Comparative Neurology

An introductory laboratory
course on the form, function
and structural interpretation
of the nervous system

With 315 illustrations

By JAMES W. PAPEZ

Cornell University

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COMPARATIVE NEUROLOGY

Nihil est in intellectu quod
non fuerit prius in sensu.

COMPARATIVE NEUROLOGY

A MANUAL AND TEXT FOR THE STUDY OF THE NERVOUS SYSTEM OF VERTEBRATES

BY

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PREFACE

This text has grown out of the needs of the laboratory course in comparative neurology given at Cornell University, Ithaca, New York. Its aim has been to provide an introductory laboratory course on the form, structure and functional arrangements of the nervous system, for students of biology, physiology, psychology and those preparing for the study of the medical sciences. In parts one and two, special consideration has been given to the structure of the mammalian brain in which the conduction systems are most completely organized. Part three is devoted to the nervous systems of the lower vertebrates, fishes, amphibia and reptiles. The evolution towards the mammalian type is indicated. The lower forms provide suitable material for the study of many fundamental problems dealing with the biological significance of the primitive neural structures.

The chapters have been arranged to provide a graded course on a limited amount of simple laboratory materials which can be easily procured: (1) formalin preserved brain of a rabbit, cat, dog, sheep or man, (2) a single series of Weigert sections of cat or some other mammal, and (3) formalin preserved head of a shark to which may be added decalcified frogs and heads of turtle and fowl.

The illustrations are intended to guide the student in identification of tracts, nuclei and other structures. The schemes illustrate the plan of connections of some of the larger fiber systems. In practice it has been found necessary to supplement these with lantern slides from other sources.

The references to literature are by no means complete. The names of larger text books and monographs are briefly given, from which the student will be able to get additional detail and general information, particularly on embryology, cell structure and physiology. The research worker and graduate student should consult the bibliographies in these works for further references.

The material for this manual has been drawn from many additional sources besides those mentioned in the bibliographies. Due acknowledgment is made to the many distinguished scholars and to earnest contributors of the younger generation.

A large number of the illustrations were drawn from original preparations made by the author. To Mrs. Pearl Papez, who drew most of the original figures, my best thanks are due. Drawings of the Primate brains from the Wilder collection and of the Carnivora were made by Mr. D. Soloway. Figures taken from other sources have been duly accredited. My grateful thanks are due to the publisher, Thomas Y. Crowell Company, whose resources and enterprise have made the publication of this work possible; and to the J. S. Cushing Company for the excellent typography.

James W. Papez

Cornell University
Ithaca, New York
January, 1929

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ABBREVIATIONS FOR ALL FIGURES

a,	axone
ab,	abducens nerve
ac,	anterior commissure
acc,	accessory portion of spinal accessory nerve
acn,	accessory cuneate nucleus, or nucleus of restiform body
aepf,	outer pillar cell
af,	arcuate fibers
al,	alar or central lobule
alv,	alveus or fibers on inner surface of hippocampus (angular bundle)
am,	ambiguus nucleus
amy,	amygdalar region
an,	abducens nucleus
ang,	angular bundle, piriform-hippocampal, forms (*hc*)
ans,	ansiform or semilunar lobule
ansa,	ansa lenticularis
ant,	anterior nucleus of the thalamus
aon,	accessory olfactory nerve
ap,	ansa peduncularis
apt,	anterior peduncle of the thalamus
aq,	cerebral aqueduct
ar,	auditory radiations
arc,	arcuate or ventrolateral nucleus of the thalamus, or arcuate fibers
arn,	arcuate nuclei of oblongata
as,	acoustic stria
aso,	accessory superior olive
at,	acoustic tubercle or dorsal cochlear nucleus
av,	anterior medullary vellum
b,	basket or stellate cells
bc,	brachium conjunctivum
bcx,	decussation of brachium conjunctivum
bi,	bigeminal body or tegmental area
bic,	brachium of the inferior colliculus
bip,	bigeminal pontal tract
biv,	biventral lobule
bon,	basal optic nucleus (supraoptic)
bp,	brachium pontis
bulb,	oblongata
c,	central canal
c1,	first cervical nerve
cap,	capillary
cat,	central acoustic tract
cb,	cerebellum
cbc,	cerebellar crest over lateral line lobe
cdn,	caudate nucleus
cen,	central nucleus of dorsal horn
cer,	cerebrum
cg,	central gray
ch,	cortico-habenular tract
chp,	choroid plexus
cf,	central tegmental fasciculus
cic,	commissure of inferior colliculus
cil,	ciliary nucleus
cing,	cingulum
cl,	clivus of cerebellum
cli,	climbing fibers of cerebellum
cll,	commissure of lateral lemniscus
cn,	cuneate nucleus
cnt,	central nucleus, or centrum medianum of the thalamus, also called posterior nucleus of the thalamus
co,	cochlear nerve
cp,	cerebral peduncle
cpo,	cerebro-pontal tract
cr,	cerebellar root of vestibular nerve
cs,	cerebro-spinal (pyramidal) tracts
csc,	commissure of superior colliculus
cst,	cortico-epistriate tract of Birds and Reptiles
ct,	subcallosal fasciculus (subependymal)
cul,	culminate or anterior lunate lobule
cv,	cerebellar vermis
cvm,	crossed vestibulo-mesencephalic tract
cvr,	crossed vestibular root
cvs,	crossed vestibulo-spinal tract
d,	dendrite
db,	diagonal band or olfacto-septal fibers (*ols*)
dbc,	descending limb of brachium conjunctivum

dcs,	direct cerebro-spinal tract
dd,	dorsal division of spinal nerve
df,	dorsal fasciculus of Schutz
dg,	dentate gyrus (96)
dh,	dorsal horn of cord
dm,	dorsomedial nucleus of cord
dmn,	dorsomedial nucleus of thalamus
dn,	dorsal nucleus of cord (Clarke)
don,	dorsal olivary nucleus
dor,	dorsal nucleus of the thalamus
dp,	dorsal fasciculus proprius
dr,	dorsal root
ds,	dorsal septum
dsc,	dorsal spinal cerebellar tract (of Flechsig)
dt,	descending root of trigeminal nerve
dtn,	deep tegmental nucleus (of Gudden)
dvn,	descending vestibular nucleus (of Schwalbe)
dvr,	descending vestibular root
e,	external capsule
emb,	emboliform nucleus
ep,	epithelium
et,	and
F,	fiber layer of cortex
f,	facial nerve
fas,	fastigial nucleus
fc,	fasciculus cuneatus
fcl,	fibrocellular layer of olfactory tubercle
fg,	fasciculus gracilis
fh,	hippocampal fissure
fl,	flocculus
fn,	facial nucleus
fol,	folium vermis of cerebellum
for,	foramen
forebrain,	telencephalon, cerebral hemispheres
fp,	fissura prima or preclival fissure of cerebellum
fs,	fissura secunda of cerebellum
fv,	fourth ventricle
fx	fornix
fxc,	fornix, septal or anterior pallial commissure
G,	granule layer of cortex
g,	granule cell
gang,	ganglion
gc,	geniculate, transverse or postoptic, commissure

gf,	genu of facial nerve
gl,	glomerulus, a ball like synaptic area
gn,	glossopharyngeal nerve
gp,	globus pallidus of striatum
grc,	gracile lobule of cerebellum
gt,	geniculo-tectal tract of Birds
gu,	gustatory nucleus of vagus (and *gn*)
hb,	habenular bodies
hc,	hippocampal commissure (97) or posterior pallial commissure
hg,	hippocampal gyrus (104) or subiculum (*sb*)
hip,	hippocampus and hippocampal primordium in lower vertebrates
hp,	habenulo-peduncular tract
hc,	habenular commissure
hy,	hypoglossal nerve
hyn,	hypoglossal nucleus
i,	intermediate nerve
ic,	inferior colliculus
if,	interpeduncular fossa
ifd,	infundibulum
ilf,	inferior longitudinal fasciculus
in,	intermediate nucleus
inc,	nucleus incertus
info,	infundibular organ
int,	internal capsule
intra,	intrapeduncular nucleus
io,	inferior olive
ip,	interpeduncular nucleus
is,	interstitial nucleus
isp,	interstitial spinal tract
it,	intercalate nucleus
j,	glia, ependymal or supporting cell
k,	collateral
l,	lateral line nerves of Fishes and Larval Amphibia
la,	anterior lobe of cerebellum
lat,	lateral nucleus of the thalamus
lata,	anterior lateral nucleus of the thalamus of Birds
lc,	latero-cerebellar or external arcuate fibers
lco,	lateral white column of the cord
lfb,	lateral forebrain bundle
lg,	lateral geniculate body
lh,	lateral horn or sympathetic nucleus of the cord

lin,	lingula of cerebellum
lis,	Lissauer's tract
ll,	lateral lemniscus
llsp,	spiral lamina of cochlea
lm,	middle lobe
ln,	lateral nucleus
loc,	locus coeruleus
lot,	lateral olfactory tract
lp,	lateral fasciculus proprius
lr,	lateral recess
lrs,	lateral reticular spinal tract
ls,	lateral sulcus
lspo,	spiral lamina of the cochlea
lt,	lateral nucleus of the tuber cinereum
lun,	lunate, posterior lunate or clival lobule
lv,	lateral ventricle
lvn,	lateral vestibular nucleus (Deiters')
lvr,	lateral vestibular root

M,	molecular layer of cortex
m,	motor cell
ma,	medullary area or white matter (*w*)
mb,	mammillary body
mba,	basal membrane of the cochlea
mc,	Meynert's supraoptic commissure
med,	medial nucleus of the thalamus
mes,	mesencephalic root of the trigeminus
mf,	medial longitudinal fasciculus
mfb,	medial forebrain bundle or olfacto-peduncular tract (*olp*)
mi,	massa intermedia
midbrain,	mesencephalon
midl,	middle lobe of cerebellum
mit,	mitral cell
mg,	medial geniculate body
mgs,	middle gray stratum
ml,	medial lemniscus
mlf,	medial longitudinal fasciculus
mm,	vestibular membrane
mn,	masticator nucleus or nerve
mon,	medial olivary nucleus
mp,	mamillary peduncle
mr,	motor or ventral root
mrs,	medial reticular spinal tract
mt,	mammillo-thalamic tract (Vicq d'Azyr)
mte,	tectorial membrane
mv,	dorsal motor nucleus of the vagus
mvn,	medial vestibular nucleus (Schwalbe)
mvr,	medial vestibular root

n,	peripheral processes of the cochlear nerve to the organ of Corti
nc,	cochlear nerve
nd,	nucleus dentatus of cerebellum, ventral or subcerebellar nucleus of lower vertebrates
ng,	nucleus gracilis
ngl,	nucleus globosus
ni,	nucleus or ganglion isthmi
nl,	nucleus lateralis
nll,	nucleus of the lateral lemniscus
nlf,	nucleus of the lateral fasciculus proprius of the cord
no,	nodulus of the cerebellum
not,	nucleus of the optic tract (pretectal)
npc,	nucleus of the posterior commissural (prebigeminal)
nrB,	nucleus reticularis of Bechterew
nrc,	central reticular nucleus
nro,	nucleus reticularis of oblongata
nrp,	nucleus reticularis of pons
ns,	nasal sac, and nervous system
nter,	terminal nerve
nve,	ganglion of the vestibular nerve

ob,	olfactory bulb
obr,	olivary bridge
oc,	olivocerebellar fibers, or external arcuate fibers
oh,	olfacto-habenular tract (ansa peduncularis)
ol,	olfactory lobe
olf,	olfactory cortex
oln,	olfactory nerve
olp,	olfacto-peduncular tract (strio-thalamic) or the medial forebrain bundle
ols,	olfacto-septal fibers or subcallosal gyrus
om,	oculomotor nerve
op,	olivary peduncle or olfactory peduncle
opx,	intercrossing of olivary peduncle
or,	optic radiation
os,	olivary sac of inferior olive
ost,	olfactory striatum or peduncular nucleus
ot,	optic tract

P,	layer of pyramidal cells or of Purkinje cells
p,	pyramidal cell

pa,	postansiform or postsemilunar fissure
par,	paraphyseal fold
Pc,	Purkinje cell of cerebellum
perf,	perforating fibers of angular bundle (*ang*)
peri,	peripeduncular nucleus (of Jacobsohn)
pf,	peduncle of the flocculus
pff,	parafloccular fissure
pfl,	paraflocculus
pin,	pineal body
pir,	piriform area or gyrus
pit,	pituitary body or hypophysis
pl,	postlunate or postclival fissure
pm,	paramedian lobule
pmf,	paramedian fissure
pn,	pontal nuclei
pnf,	postnodular fissure
pp,	pontal protuberance
pro,	preolivary nucleus
prom,	promontory of cochlea
ps,	pigment spot
pt,	Probst tract
pul,	pulvinar
put,	putamen
pv,	posterior medullary velum
pyr,	pyramidal lobule of the cerebellum
r,	rudiment
rb,	restiform body
rc,	reticulo-cerebellar fibers (long external arcuate fibers)
reu,	reuniens or central nucleus of the thalamus
rf,	rhinal fissure
rn,	red nucleus
rot,	nucleus rotundus of Birds and Reptiles
rs,	rubrospinal tract
rsx,	rubrospinal decussation
rt,	reticular formation of brain stem
rtt,	outer reticular zone of the thalamus
ruf,	reticular division of uncinate fasciculus
S,	layer of stellate cells of cortex
s,	stellate cell
sac,	dorsal sac
sb,	subiculum of hippocampal gyrus (*hg*)
sc,	superior colliculus or tectum
scty,	scala tympani or tympanic canal
scv,	scala vestibuli or vestibular canal
semi,	semilunar nucleus of Birds
sep,	septal region, nuclei septi, of forebrain
sf,	solitary fasciculus or descending sensory root of the vagus and glossopharyngeal nerves
sg,	substantia gelatinosa trigemini
sgs,	superficial gray stratum of the tectum
sh,	septohippocampal fibers
sl,	sulcus limitans
slf,	superior longitudinal association fasciculus
sn,	substantia nigra
snl,	subthalamic nucleus of Luys
so,	superior olive
sp,	spinal part of the spinal accessory nerve
spf,	suprapyramidal fissure of the cerebellum
spir,	spiriform nucleus of Birds
sr,	sensory radiations
st,	spinotectal tract
stc,	striocerebellar tract of Birds
sth,	spino- and bulbo-thalamic tract including the lower trigeminothalamic fibers
stn,	superior tegmental nucleus of Gudden
sto,	strio-oculomotor tract, striotegmental, or striomesencephalic tract
stp,	striopeduncular tract, striobulbar or lateral striotegmental tract or lateral forebrain bundle
sts,	striosubthalamic fibers
stz,	organ of Corti
sub,	reticular subthalamic nucleus or zona incerta
subt,	anterior medial part of (*sub*)
svn,	superior vestibular nucleus
svr,	superior vestibular root
sx,	subthalamic or supramammillary decussation between (*sub*)
sy,	sylvian sulcus
t,	trigeminal nerve
t, 1,	first thoracic nerve
tb,	trapezoid body
tc,	tuber cinereum of hypothalamus

tectum,	optic vesicles or tectum of the midbrain
teg,	lateral tegmental nucleus of midbrain
ter,	nerve terminal
tf,	thalamic fasciculus or thalamo-frontal tract of lower forms
tg,	trigeminal ganglion
th,	thalamus, diencephalon or interbrain
ths,	septothalamic tract or medial forebrain bundle
tl,	tonsilar lobule
tm,	tecto-mesencephalic tract
tmn,	tuberomammillary nucleus
tn,	trigeminal nucleus
to,	tecto-olivary or tegmento-olivary tract
ton,	tonsillar lobule of cerebellum
tp,	transverse peduncular tract
tr,	tract
tro,	trochlear nucleus or nerve
ts,	tecto-bulbar and tectospinal tract
tst,	terminal stria
tsx,	tectospinal decussation
tth,	tectothalamic tract to nucleus rotundus of Birds
tu,	tuber vermis
tub,	olfactory tubercle
uf,	uncinate fasciculus of cerebellum
ufc,	uncinate fasciculus of cerebrum
us,	uvular sulcus
uv,	uvula or uvular lobule
v,	vagus nerve
va,	sensory vagal nucleus or ala cinerea
vac,	vagal commissure
vas sac,	vascular sac
vc,	ventral commissure of the cord
ven,	ventral cochlear nucleus
vco,	ventral column of the cord
vcs,	ventral cerebrospinal tract
vd,	ventral division of spinal nerves
ven,	ventral, or ventromedial nucleus of the thalamus
vf,	ventral fissure
vh,	ventral horn
vis,	visceral nerves
vl,	ventro-lateral nucleus
vm,	direct vestibulo-mesencephalic tract
vn,	vestibular nerve
von,	ventral olivary nucleus
vp,	ventral fasciculus proprius
vr,	vestibular root
vrn,	ventral reticular nucleus
vrs,	ventral reticular spinal tract
vs,	direct vestibulo-spinal tract
vsc,	ventral spino-cerebellar tract (Gowers')
W,	white matter
x,	decussation of cerebro-spinal tract
y,	bifurcation

PART I

GROSS STRUCTURE OF THE BRAIN OF MAMMALS

COMPARATIVE NEUROLOGY

CHAPTER 1

The Cerebrum of Lower Mammals

The mammals are distinguished by the presence of a well-developed bilateral **forebrain.** This is divisible into (1) the primitive **olfactory brain** and (2) dorsal to it the non-olfactory **cerebrum.** The cerebrum of each side is as a rule clearly separated from the olfactory brain by the **rhinal fissure.** The olfactory brain, though primitive, is an organ of great importance in all the lower macrosmatic mammals in whom the function of smell is of great importance. To this has been added the non-olfactory cerebrum preeminently developed only in the higher Anthropoidea and man. We recognize the lower type of smooth brains without sulci and gyri, and the more advanced gyrencephalic types with sulci and gyri. Examine first a number of smooth brains of some of the lower orders.

In the lowest order of mammals, the Monotremata, the forebrain is of relatively large size. Figures 1, 49, 50 and 51 illustrate the brain of a monotreme, the duck-billed platypus (*ornithorhynchus anatinus*). It will be seen that the cerebral hemispheres (*cer. hem.*) of this lowly mammal are formed by an expanse of cortex smooth and oval in shape, with narrow frontal ends. In front and on the ventral side are the olfactory bulbs (*olf. b.*) and behind is the cerebellum (*cer.*); neither of these is covered by the cerebral cortex. The only furrows in the cerebrum are those produced by the middle and anterior cerebral arteries and large veins (*v. cereb. mag.*) that converge towards the apex of the hemisphere. The posterior temporal region is indented by the large floccular lobe (*floc.*) of the cerebellum.

To account for this large cerebrum one naturally looks to the sensory nerves that are known to have definite afferent connections with the cortex. According to Dubois there is among the lowly organized mammals a definite relationship between the size of the cortex and the extent of the various sensory surfaces of the body. In the case of the platypus the optic nerves are small, and the auditory nerves are of moderate size, but the trigeminal nerves are enormous (fig. 49). The chief tactile organ of this animal is its expanded bill-like snout with which it seeks for its food in muddy water. This snout is covered by a soft skin containing peculiarly modified sense organs richly supplied by branches of the trigeminal nerves.

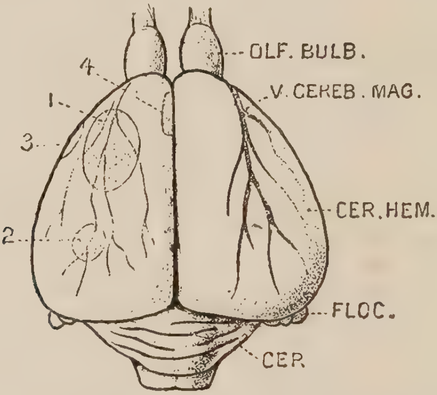

FIG. 1. Brain of a duckbilled platypus, dorsal surface, × 1⅓. After G. E. Smith.

This, however, does not fully explain the large cortex, for, in another family of the Monotremata, the echidna or spiny anteater (fig. 2), the bill and trigeminal nerves are relatively smaller and none of the other nerves are remarkable for their size, yet the cortex is very large and greatly convoluted. The remarkable resemblance of this convolutional pattern to that of Primates (compare fig. 24) deserves notice as it brings out the importance of head shape as a dominant mechanical factor in the formation of fissural patterns. The round birdlike head of this animal should be kept in mind. "The sulci of the neopallium (cerebrum) of the spiny anteater vary considerably in different individuals, and there is no clue to indicate whether any of them should be regarded as the representative of a sulcus of other mammalian brains. On the other hand the arrangement of the sulci suggests that they might be due to purely mechanical factors operating in an uniformly growing pallium, the longitudinal expansion of which is restricted." (G. E. Smith.)

The next to the lowest order of mammals, the Marsupialia, is represented by the brain of the opossum (*Didelphys v.*) in figures 3 and 53. It closely resembles the brains of perameles and the dasyuridae, that is, other small and lowly developed marsupials. The cerebral hemispheres (fig. 3) are oval and somewhat elongated vesicles covered by a highly vascular cortex. On the lateral side a well-defined **rhinal fissure** (*rf*) separates the cerebrum from the large pyriform lobe (*pir*). Posteriorly the rhinal fissure is incomplete so that the pyriform lobe and the cortex are freely united. The fissure (*rf*) is placed far dorsally as compared with its position in higher mammals, and the actual size of the cerebrum is much smaller than appears to be the case from a dorsal view. Note that the cerebrum does not cover the large olfactory bulbs (*olf b*) in front and that posteriorly the cerebellum is wholly uncovered and even parts of the quadrigeminal bodies are seen between the cerebellum and occipital lobes. At the front end a shallow depression in the cortex may represent an incipient presylvian sulcus (3). Many small vascular grooves run across the cortex.

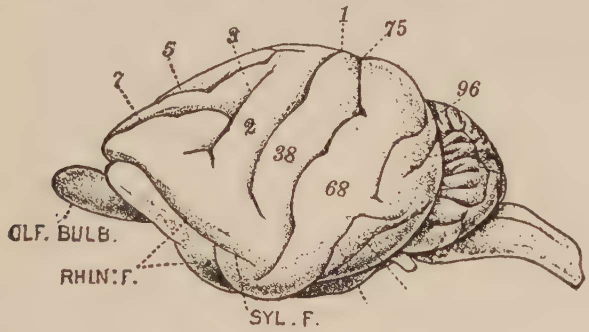

FIG. 2. Brain of a spiny anteater, lateral view, × 1¼. After G. E. Smith.

The great size of the olfactory bulbs and pyriform lobe and of the olfactory tubercle on the ventral side (fig. 53) clearly shows the macrosmatic nature of this brain. The opossum's choice of putrid food and fossorial habits naturally lead to the great expansion of the olfactory brain, and in spite of its semiarboreal habits the optic centers and cerebral cortex show no special indication of development in the visual and motor areas.

In the Insectivora in general the forebrain is small and smooth. The olfactory parts are well developed, but the cerebrum is of small size. The brain of the small arboreal flying lemur, colugo (*galeopi-*

thecus volans) is of special interest because, though primitive and highly macrosmatic, it presents a series of well-defined cerebral sulci (figs. 4 and 5). On the dorsal surface is a longitudinal sulcus (*w*) which according to G. E. Smith resembles the conjoint suprasylvian and coronal sulci of some small Ungulates. On the lateral surface are seen the short presylvian sulcus (*x*) and the sylvian sulcus (*y*). On the medial surface in the occipital region there is a deep calcarine (splenial) sulcus, and another sulcus cuts the medial margin of the frontal pole.

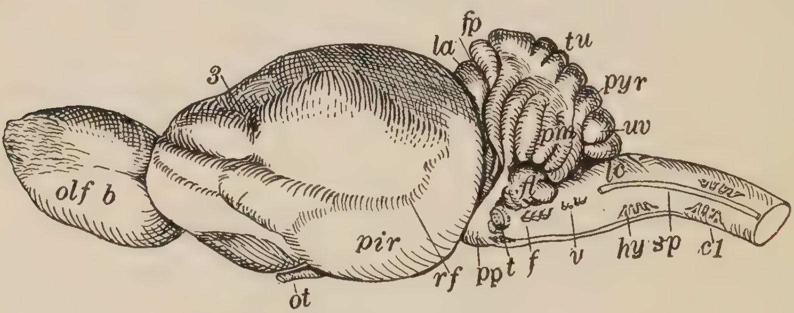

Fig. 3. Brain of an opossum, lateral view, × 2.

The order of Rodentia that includes so many groups of smaller mammals presents a degree of cerebral development somewhat higher than that of the opossum and other smaller Marsupials. The same may be said of the small Insectivora, such as the hedgehog, and the smaller Edentata, such as the armadillo (fig. 54). The fossorial habits of these small animals and their dependence on the olfactory sense in search of food accounts for the high degree of development of the olfactory brain. This mode of life has not favored in most cases the expansion of the visual and other sensory and motor areas of the cerebral cortex.

Examine the brain of a rabbit (figs. 6, 7, 8, 9) and compare with that of a marmot (fig. 62) and armadillo (fig. 54). Note the long curved **rhinal fissure** (*rf*) which separates the cerebrum from the pyriform lobe (*pir*). In the herbivorous rodents, such as the rabbit and marmot, its position is more on the ventral side as compared with its position in the primitive opossum and the more grovelling and mascrosmatic hedgehog and armadillo. The rabbit and marmot depend to a larger extent on their eyes and ears in seeking for food, shelter and protection from enemies, and their cerebrum shows a slight preponderance over the olfactory brain.

The hemispheres are oval and taper at their frontal ends which project somewhat over the olfactory bulbs (*olf b*). The occipital pole (visual area) is somewhat enlarged and conceals almost completely the quadrigeminal bodies (*sc*, *ic*) and the anterior lobe of the cerebellum. The temporal lobes are large enough so that in a dorsal view (fig. 8) they quite conceal the pyriform lobes. A small amount of ventral flexion is seen in the pyriform areas (fig. 7). On the dorsal surface, running parallel to the sagittal fissure, is seen a shallow lateral sulcus (fig. 8, *ls*). The slight bulging of the occipital lobes seen in hardened rabbit brains is often circumscribed by a shallow depression. From figure 195 it will be seen that this depression would correspond to the lateral margin of the visual area 17; and that the lateral sulcus runs along its dorsal margin between the areas 18 and 29d. On the medial surface of the frontal lobe (fig. 6) is a shallow depression corresponding to the region of area 24. A study of figures 195 and 196 at once reveals the high degree of cellular differentiation of the cortex of the rabbit. Among other features the frontal areas 6 and 8 are notably deficient.

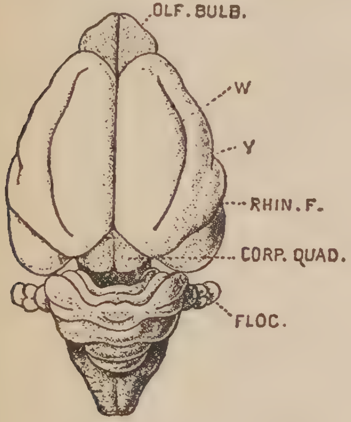

FIG. 4. Brain of a colugo, dorsal view, × 1¼.

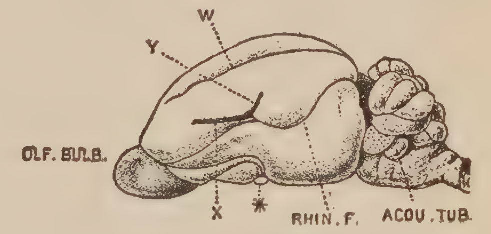

FIG. 5. Brain of a colugo, lateral view, × 1¼. After G. E. Smith.

In a median section of a rabbit brain (fig. 6) note the presence of a definite corpus callosum (*cc*) which is practically absent in the platypus (fig. 51), kangaroo (fig. 52) and opossum. Note how its anterior end over-arches the diagonal band or parolfactory area (32). The presence of the corpus callosum is correlated with the higher degree of differentiation of the cerebrum. Its greater size is a mark of superiority in cerebral organization.

Mammals exhibit a wide range of adaptation to a terrestrial as well as aquatic mode of life. Their success depends in no small measure on the presence of the relatively new structure, the non-olfactory cerebral cortex. This highly developed expanse of nervous tissue has arisen from the dorsal wall of the older and more primitive olfactory brain.

The origin of the cerebrum in the lower mammals is correlated with the ingrowth into this dorsal wall of fibers from the lower sensory centers. The lower centers of cutaneous and deep sensibilities, the visual and auditory centers become in this way connected with special areas of the cerebrum into which they discharge the sensory impulses in all their varying modalities. Thus the cerebrum has become a manifold receptive center into which the sensory experiences are continuously irradiated and there undergo refined analysis. To what extent animal behavior, intelligence and sentiment can be compared with the conscious processes of the human mind is uncertain, but in regard to crude sensory experiences they are probably similar. Pavlov and his co-workers have shown that in animals the cerebral cortex is an organ in which there exists the mechanism

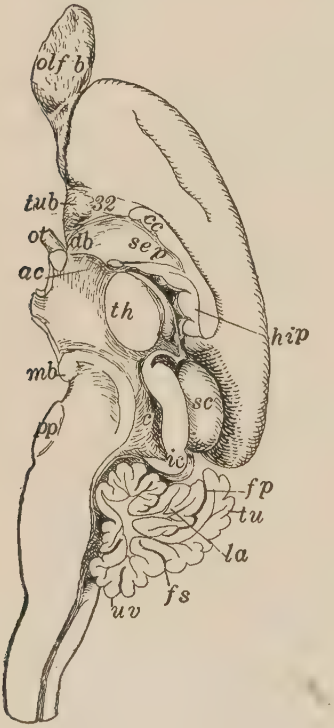

FIG. 6. Brain of a rabbit, medial view of right half, × 1¾.

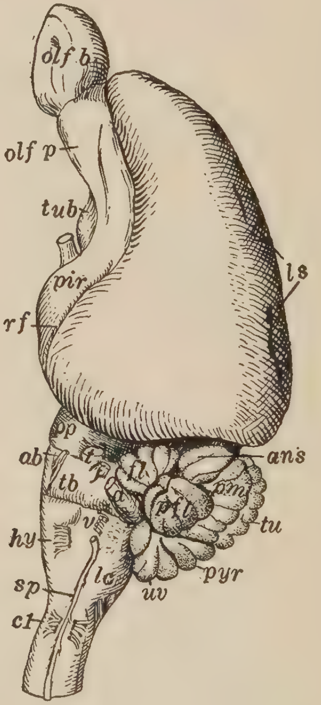

FIG. 7. Brain of a rabbit, lateral view, × 1¾.

for the formation of new associations or temporary connections of any of the afferent sensibilities with various motor responses which in turn can modify or adapt the reflex movements to a changing environment. For this adaptative function the cortex is essential, since with its removal this function ceases.

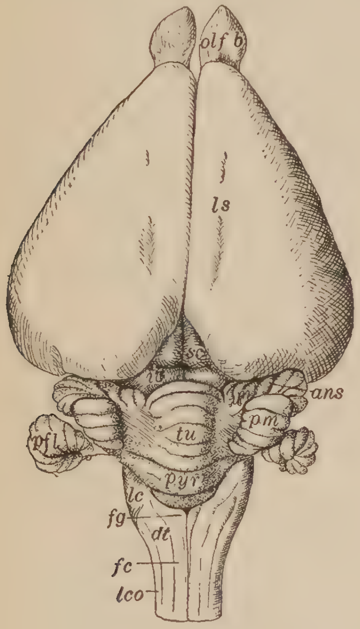

FIG. 8. Brain of a rabbit, dorsal view, × 1¾.

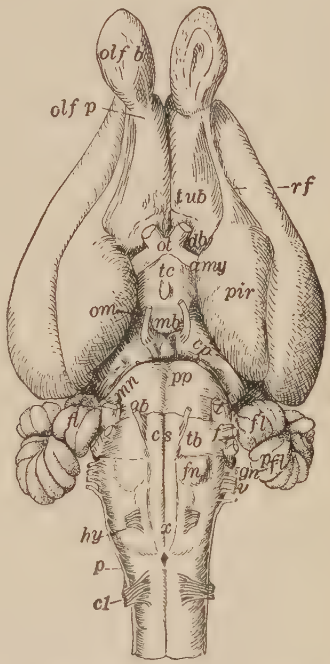

FIG. 9. Brain of a rabbit, ventral view, × 1¾.

For explanation of lettering see page xxi.

Acquaint yourself now with the various orders of Mammals.

MONOTREMATA, e.g. duckbilled platypus, spiny anteater.
MARSUPIALIA, e.g. opossums, bandicoots, wombats, kangaroos.
EDENTATA, e.g. manis, armadillos, sloths, anteaters.
CETACEA, e.g. whales, killers, porpoises, dolphins.
SIRENIA, e.g. dugong, manatee.
UNGULATA, e.g. hyrax, pigs, tapirs, rhinoceroses, horses, cattle, sheep, hippopotami, elephants.
CARNIVORA, e.g. cats, dogs, bears, weasels, otters, seals, walruses.
RODENTIA, e.g. mice, rabbits, squirrels, beavers, porcupines.
INSECTIVORA, e.g. moles, shrews, hedgehogs.
CHIROPTERA, e.g. flying foxes and bats.
PRIMATES, e.g. lemurs, marmosets, monkeys, apes and man.

CHAPTER 2

THE CEREBRUM OF THE CAT

EXAMINE the forebrain of a cat. Remove the covering membrane or pia with its blood vessels from the surface of the brain. Do not remove the pia from the medial surface or from the basal surface of the occipital lobe at this time. Note how it is folded into the sulci carrying blood vessels with it. Unless great care is taken the cerebral surface will be broken or torn in drawing the pia and arteries out of the sulci.

The **forebrain** consists of a right and a left **hemisphere** separated on the dorsal side by the longitudinal cerebral fissure which, in the brain case, is occupied by a sickle-like partition of dura mater, the cerebral falx. The forebrain is divided into the dorsal **cerebrum** and ventral **olfactory brain.** The term **cerebrum** is here used to denote the greatly convoluted cortex devoted to the reception and correlation of the impulses of vision, hearing, cutaneous and deep sensibility and volitional motor impulses. A rudiment of the cerebrum is apparent in Reptiles, but it reaches its greatest development in mammals, particularly in the Primates and man. The term **olfactory brain** is used to designate the more primitive forebrain with its olfactory cortex, such as the preterminal area (32), pyriform lobe and hippocampus, seen on the ventral and medial surfaces. This is more ancient than the cerebrum of mammals since it is found in Fishes, Amphibians and Reptiles. The olfactory brain of these lower vertebrates is a fundamental tubular structure from the dorsal wall of which the cerebrum has arisen and upon which it is superimposed in mammals.

The cerebrum of the cat, dog and other large mammals is gyrencephalic presenting a definite arrangement of sulci and gyri in each group of animals.

The **cerebral cortex** is the external coating of gray, cellular matter seen on the surface of the forebrain. It is spread as a thin layer over the internal layer of white substance, the medullary center of the cerebral hemispheres. In higher mammals the cortex is folded in many places, forming the **gyri** or outward folds that appear on the surface and the **sulci** or inward folds, which, on account of compression of their sides, have their cortex largely hidden from view. The infoldings that involve the cortex, medullary center and the ventricular (internal) surface are spoken of as **fissures.** The cortex that covers the gyri and sulci is everywhere continuous and is folded over leaflike extensions of the medullary center. The latter consists of myelinated fibers that enter or leave the cortex, and make distant connections.

Identify the **rhinal fissure** (93) on the lateral surface of the forebrain by comparing with figures 10 and 11. Its anterior part separates the olfactory tracts (14) from the frontal lobe and its posterior part separates the pyriform area (66) from the temporal lobe. It is a very fundamental fissure which in all the lower macrosmatic mammals marks the boundary between the basal olfactory cortex or pyriform area and the newer cerebral cortex dorsal to it. In lemurs, monkeys and man (Primates) on account of the reduction of the olfactory cortex and the great lateral expansions of the cerebrum the anterior part of the rhinal fissure is effaced.

In the cat the cerebral cortex is moulded by a definite though simple pattern of sulci and gyri. They represent a fairly stable though simple condition of the forebrain development of the Carnivora in general. In these animals the brain attains much larger dimensions in proportion to the size of the animal than is the case in Rodents, Edentates and Insectivors, and this increase is due to the larger size of the cerebrum. This renders the olfactory bulbs and centers less prominent, though they are still large and well defined and important functionally (macrosmatic). Hence, we find in the cat's brain that the rhinal fissure is low down on the lateral surface and partly on the ventral surface of the hemisphere.

The **crucial sulcus** (5) cuts the dorso-medial border of the hemisphere so that it presents a lateral and medial limb on the corresponding surfaces. The large *S*-shaped gyrus in front of it is the **anterior sigmoid gyrus** (2) and the one behind it is the **posterior sigmoid gyrus** (4). Curving around the lateral limb of the sigmoid gyri is the **coronal sulcus** (1). Ventral and posterior to this is the coronal gyrus (38). Great importance is attached to the coronal sulcus (1) since from histological studies and physiological experiments it appears that it separates the **motor area** which surrounds the lateral end of the crucial sulcus (5) from the **area of deep sen-**

sibility which is lateral and posterior to the coronal sulcus in the **coronal gyrus** (38).

A common and interesting variation of the coronal sulcus is seen in figures 10 and 11. Its posterior end may join the anterior end (ansate sulcus, 39) of the lateral sulcus as in figure 11; or it may end by turning dorsally in front of the bifurcation of the lateral sulcus (ansate, 39) and a shallow depression (1b) may be seen in the posterior sigmoid gyrus (4). This sulcus (1b) appears to carry the cleavage between sensory and motor areas somewhat more dorsally into the hind limb area.

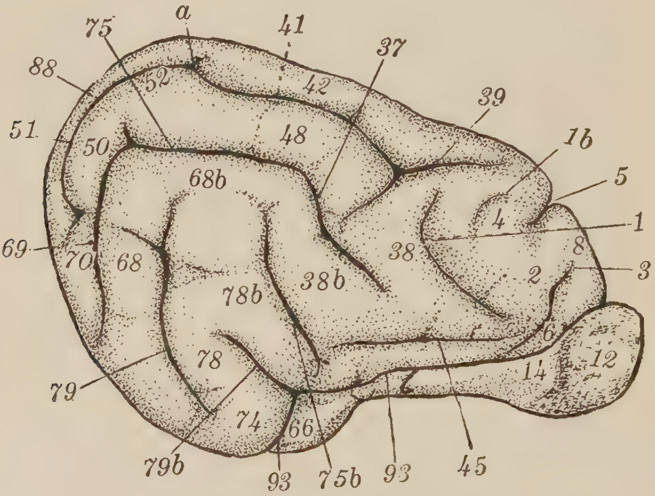

Fig. 10. Cerebrum of a cat, lateral view, × 2. For explanation of numbers see page 26.

The **presylvian sulcus** (3) (orbital) is a deep cleft in front of the coronal and anterior sigmoid (2) gyri. This sulcus occurs at the anterior limits of the motor and deep sensibility areas. The medial end of the anterior sigmoid gyrus (2) turns forward around the dorsal end of the presylvian sulcus (3) to be continuous with the **frontal gyrus** (8) dorsal to the olfactory bulb (12).

The **diagonal sulcus** (45) is seen ventral to the coronal gyrus (38) running somewhat parallel with the anterior rhinal fissure. Its posterior end may or may not join the anterior ectosylvian as in figures 10 and 11. The olfactory bulb (12) and stalk (14) lie close under the frontal gyrus and sometimes there is seen here a slight indentation which corresponds to the prominent **olfactory sulcus** (21) (rectus) seen in the dog and other Carnivora.

The **frontal lobe** may be defined as constituting all the cortex medial and in front of the coronal sulcus. It is notably small in the cat.

The **sylvian sulcus** (79b) in the cat is a short one that cuts the lateral and ventral surface of the cortex obliquely, dorsally and backwards in front of the temporal pole. Its ventral end joins the posterior rhinal fissure (93). Its dorsal end is always independent. It is bounded in front and behind by the **anterior** (78b) and **posterior** (78) **sylvian gyri** which coalesce above to form the **middle sylvian gyrus** (78). It is a distinctive feature of feline brains that this usually passes dorsally into the middle ectosylvian gyrus, but often small secondary depressions indicate a tendency to separation, as in figure 10. The **anterior sylvian gyrus** (78b) is often reduced in size.

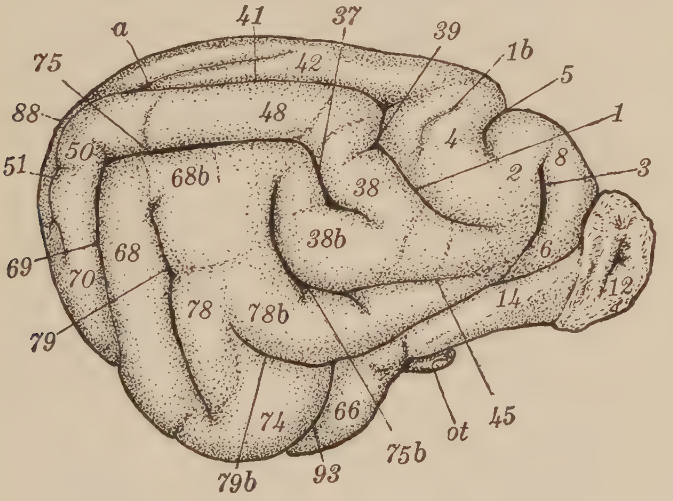

FIG. 11. Cerebrum of a cat, lateral view, × 2.

The **anterior ectosylvian sulcus** (75b) is an oblique furrow in front of the anterior sylvian gyrus. Its forward end may join the diagonal sulcus (45) as in figure 11 or may end behind it as in figure 10. The **anterior ectosylvian gyrus** (38b) is in front of the sulcus. Its fore end joins the coronal gyrus, and together they exhibit a tendency to overgrow the diagonal and anterior ectosylvian sulci so that the anterior ectosylvian gyrus often appears to be pushed in a backward direction.

The **posterior ectosylvian sulcus** (79) is an independent, almost vertical furrow back of the posterior sylvian gyrus. Often its dorsal end curves forward towards the anterior ectosylvian. Though they rarely unite in the cat, a narrowing of the interval and shallow depressions between them are often seen. The cortex above this narrowing is designated the **middle ectosylvian gyrus** (68b). The cortex behind the sulcus is the **posterior ectosylvian gyrus** (68). The sylvian and posterior ectosylvian cortex represents in a general way the **temporal lobe.** It includes the auditory area and its surrounding cortex.

The **suprasylvian sulcus** (75) is a long arched furrow that surrounds the ectosylvian cortex. It is divisible into a vertical

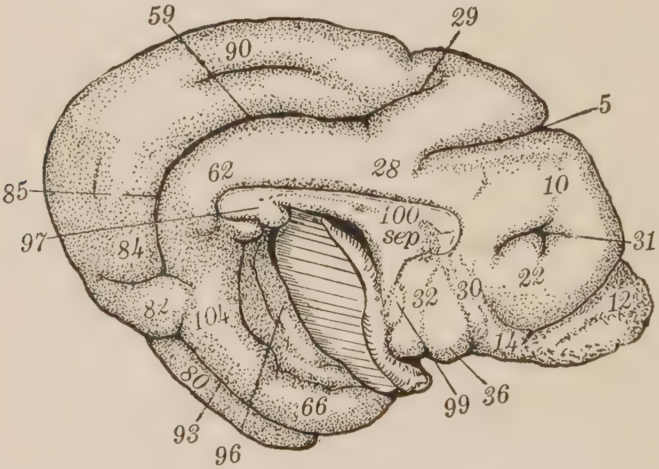

Fig. 12. Cerebrum of a cat, medial view of left half, × 2.

postsylvian sulcus (69), a horizontal **middle suprasylvian sulcus** (75) and a short curved **anterior suprasylvian sulcus** (37), which ends behind the coronal gyrus (38). The **suprasylvian gyrus** (48) describes an extensive curve posterior and dorsal to the sulcus and is divided into posterior, middle and anterior parts. The coronal gyrus (38) forms the posterior boundary of the coronal sulcus (1). The **middle suprasylvian gyrus** (48) has a long horizontal extent dorsal to the middle suprasylvian sulcus. The **posterior suprasylvian gyrus** (50) extends vertically towards the lower occipital margin but is often cut short by a forward curve of the **posterior lateral** sulcus (51) as in figure 10.

The **lateral sulcus** (41) runs horizontally on the dorsal surface and separates the middle suprasylvian gyrus (48) from the **lateral gyrus** (42) which forms the medial dorsal border of the hemisphere.

The front end of the lateral sulcus (ansate sulcus, 39) bifurcates and forms the posterior boundary of the posterior sigmoid (4) and coronal gyri (38) as in figure 10. The lower limb of this bifurcation (ansate sulcus, 39) is often nearly confluent or confluent with the coronal sulcus (1) as in figure 11. The variation here is interesting because the posterior sigmoid gyrus contains the sensomotor areas for the hind limb. The slight **postcrucial sulcus** (1b) possibly indicates a separation into an anterior motor area and posterior deep sensibility area for the hind limb, just as the well-formed coronal represents a separation of these areas for the fore limb. The anterior end of the lateral gyrus (42) exhibits evidence of compression by a slight kink on its medial side (fig. 12). The **parietal lobe** may be defined as comprising the cortex of the lateral (42) and suprasylvian (48), coronal (38) and anterior ectosylvian (38b) gyri. Its function is not well known; but this is the region in which areas of cutaneous and deep sensibility are situated.

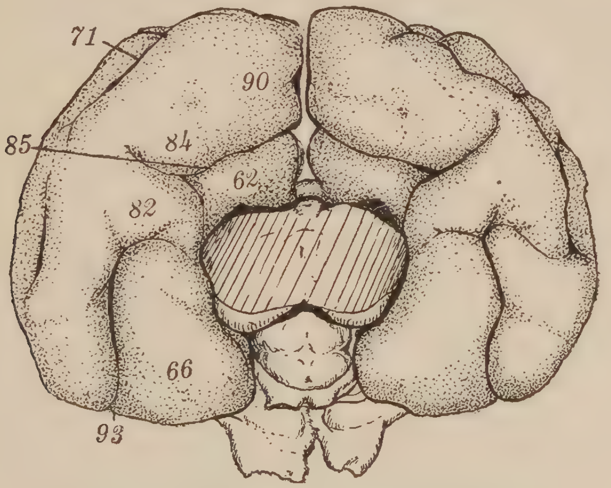

FIG. 13. Cerebrum of a cat, posterior view, × 2.

The **posterior lateral sulcus** (51) curves parallel to the occipital pole and often appears as a ventral continuation of the posterior end of the lateral sulcus as in figure 10, but its separateness in most cases is evident for its anterior end extends medial to the posterior end of the lateral sulcus as in figure 11. Thus a narrow connecting gyrus is usually seen at *a*. The **posterior lateral gyrus** (88) is the cortex medial to the sulcus. It forms the medial border of the occipital pole of the brain.

The **medial surface** (fig. 12) of the hemisphere is flat where it is compressed along the midline but posteriorly the hemispheres are widely separated by the midbrain and cerebellum. They are connected by three bands of fibers, the corpus callosum (100) which unites the hemispheres and the hippocampal (97) and anterior commissures (99) which unite the hippocampi and the basal olfactory regions. These three commissures have been cut across in the median section (fig. 12) and the brain stem has been removed to expose the hippocampal formation. In figure 13 the cerebellum and midbrain have been removed to expose the posterior medial surface of both hemispheres.

The **posterior rhinal fissure** (93) separates the lower limb of the posterior ectosylvian gyrus from the pyriform lobe. It bifurcates at its upper end and forms the ventral boundary of a **hippocampal fusiform gyrus** (82) which connects the **hippocampal** gyrus (104) with the lower end (70) of the posterior suprasylvian gyrus. The calcarine sulcus (85) begins above this gyrus and curves upward and forward cutting very deeply into the medial wall of the hemisphere. The anterior part is continued as the **intercalary sulcus** (59) dorsal to the middle of the corpus callosum. Its anterior end curves up behind the medial limb of the **crucial sulcus** (5) which cuts the dorsal border in a horizontal direction above the front end of the corpus callosum. The calcarine sulcus (85) separates the **parasplenial gyrus** (62), which curves over the posterior end of the corpus callosum, from the **suprasplenial gyrus** (90). In the latter a shallow **anterior suprasplenial sulcus** (89) is seen and the suggestion of a **postcalcarine sulcus** is seen back of the calcarine. This cortex above and back of the calcarine sulcus is the visual area. It forms the border of the occipital pole and is limited by the posterior lateral sulcus (51) on the lateral surface.

Where the **crucial sulcus** (5) cuts the medial surface, the sigmoid gyri turn over the medial border to form its boundaries. The anterior one (2) is continued forward into the superior frontal (10). The posterior one joins the medial parietal gyrus. The medial frontal surface has a faint **genual sulcus** (31). The surface ventral to the front end of the corpus callosum and in front of the anterior commissure is the **subcallosal gyrus** and **diagonal band** (32).

CHAPTER 3

The Cerebrum of the Dog

Examine the forebrain of the dog. Carefully remove the pia from the lateral surface so that the sulci may be opened to expose the depth of their cortex. In comparing the forebrain of the dog (figs. 14–17) with that of the cat, the fundamental similarity of the gyral pattern is soon recognized. The brain of the dog is larger; the cortex is more developed and a crowding of gyri and many secondary sulci make the cerebral pattern of the dog appear more complex. The brain is strongly macrosmatic, possessing large olfactory bulbs, stalks and secondary olfactory cortex at its base. For the following systematic examination consult the figures.

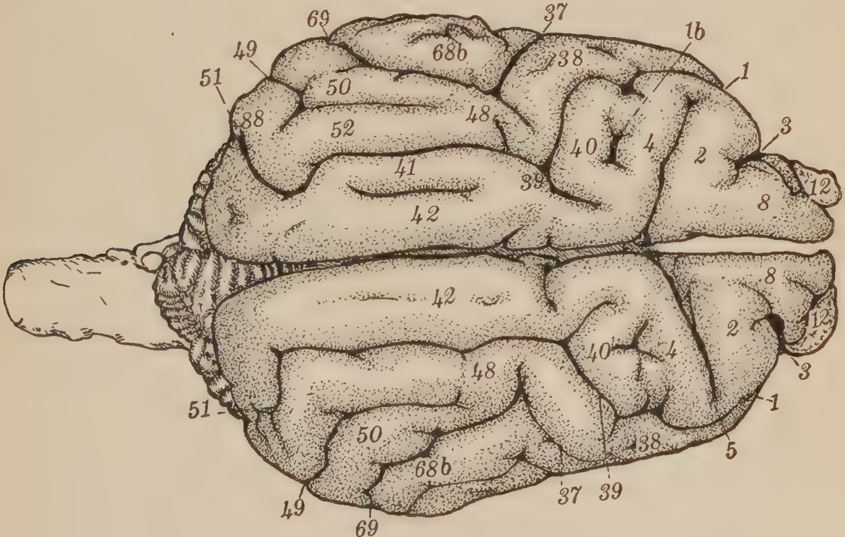

Fig. 14. Cerebrum of a dog, dorsal view, × $1\frac{1}{3}$.
For explanation of numbers see page 26.

The **anterior** and **posterior rhinal fissures** (93) separate the cerebrum from the pyriform lobe (66). The **crucial sulcus** (5) is prominent and sometimes its lateral end is bifid. The **anterior sigmoid gyrus** (2) is thick and often indented by a shallow sulcus. Its medial end turns forward into the **frontal gyrus** (8) which also may be thick and indented by a shallow depression. The (orbital) **presylvian sulcus** (3) is a very deep cleft that separates the frontal gyri (6, 8) from the anterior sigmoid (2) and from the coronal gyrus (38) which project over it (3) as an opercular formation. When the olfactory bulb (12) is drawn down, an **olfactory sulcus** (21) is exposed in the ventral aspect of the frontal cortex.

The **posterior sigmoid gyrus** (4) is thick and depressed by a shallow **postcrucial sulcus** (1b) as in figures 14 and 15 or completely cleft by it as in figure 16. The **coronal sulcus** (1) is a deep cleft of submerged cortex that surrounds the lateral ends of the sigmoid gyri (2 and 4) which contain the motor area and separates them from the **coronal gyrus** (38) which contains the area of deep sensibility. The posterior end of the coronal sulcus (1) may join the **ansate** (39) as in figure 14. Thus the coronal gyrus (38) may appear to join the posterior sigmoid (4) or the middle suprasylvian gyrus (48) as the case may be.

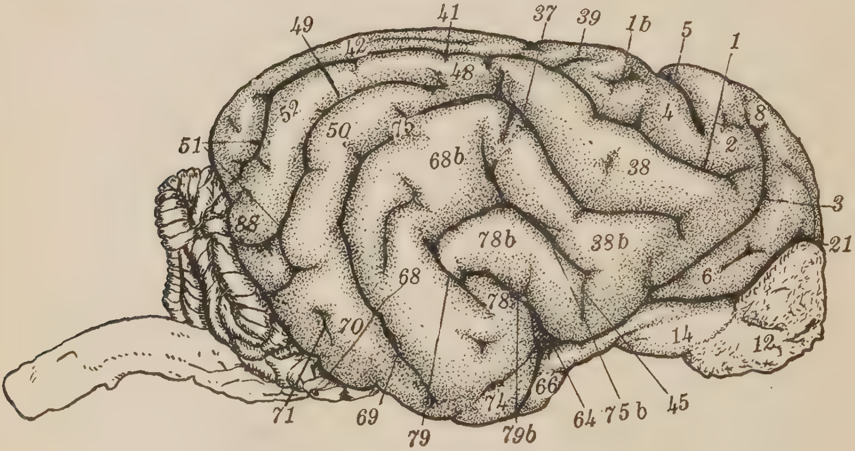

FIG. 15.—Cerebrum of a dog, lateral view, × 1⅓.

The cortex of the crucial, sigmoid, coronal, presylvian and frontal formations may be regarded as constituting the frontal lobe.

The **sylvian sulcus** (79b) joins the rhinal fissure (93) at its flexure, and for a short distance deeply cleaves the temporal cortex. It lies between the anterior (78b) and posterior (78) sylvian gyri. If these are separated, it will be seen that they are not united but cover over a triangular **insular area** (64) joined to the cortex of the pyriform lobe (66) at the bottom of the rhinal fissure. The **anterior sylvian gyrus** (78b) is large and forms an operculum over the anterior part of the insular area. Its front end is continuous with the opercular formation bounding the presylvian sulcus. The **posterior sylvian gyrus** (78) is a narrow one, depressed and drawn in over the back part of the **insular area.** Its lower end is united with the **temporal polar gyrus** (74) which forms the curved tip of the temporal pole and is separated from the pyriform lobe by the posterior rhinal fissure (93).

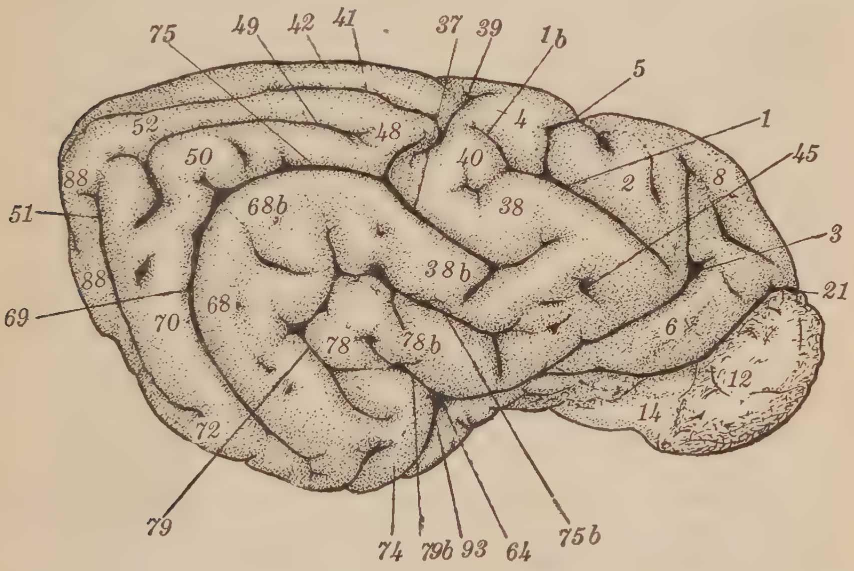

FIG. 16. Cerebrum of a dog, lateral view, × 1½.

The **ectosylvian sulcus** (79) separates the sylvian gyri (78) from the ectosylvian (68) and is divisible into anterior, posterior and middle parts. The **anterior ectosylvian sulcus** (75b) is deep and ends in the ventral part of the opercular formation. The corresponding gyrus (38b) is narrow and also ends in this formation. The **middle ectosylvian sulcus** is short, often shallow and irregular, due to small gyri that tend to cross it. The **middle ectosylvian gyrus** (68b) is broad and irregular and often united with the depressed middle sylvian gyrus (78) as in the cat. The **posterior ectosylvian sulcus** (79) is not always complete at its lower end so that the posterior sylvian and ectosylvian gyri appear incompletely separated as in figure 15. The **posterior ectosylvian gyrus** (68) is thick and ends behind the temporal polar sulcus.

The **suprasylvian sulcus** (75) is a deep cleft that cuts a sharp boundary around the ectosylvian formation separating it from the suprasylvian gyri (50 and 48). It consists of three parts. The **postsylvian sulcus** (69) takes a downward and forward course ending behind the temporal polar sulcus. The corresponding gyrus (70) behind it forms the lower part of the occipital border being limited medially by the **posterior lateral sulcus** (51). The **middle suprasylvian sulcus** (75) is a forward continuation of the posterior one (69). The corresponding gyrus (48) is narrow and is joined with the posterior suprasylvian gyrus (50) where it ends behind the **ansate sulcus** (39) in a sharp flexure which joins the **coronal gyrus** (38). The **anterior suprasylvian sulcus** (37) is a curved furrow that surrounds the lateral surface of the coronal gyrus (38) and ends anteriorly in the opercular formation.

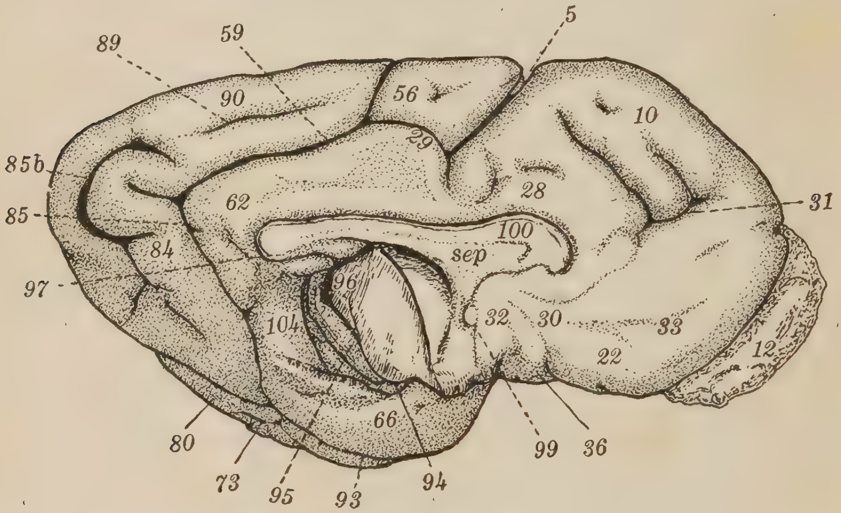

FIG. 17. Cerebrum of a dog, medial view of left half, $\times 1\frac{1}{3}$.

The cortex of the sylvian, posterior ectosylvian, polar and posterior suprasylvian formations may be regarded as constituting the **temporal lobe.** Its chief significance lies in the fact that the auditory area is located in the posterior sylvian gyrus; being surrounded by the great ectosylvian gyrus for which the suprasylvian serves as a sulcus limitans.

The **ectolateral sulcus** (49) is a new furrow in the suprasylvian region that partly separates the suprasylvian gyrus (50) from the new ectolateral gyrus (52). Though often a single cleft, it may be

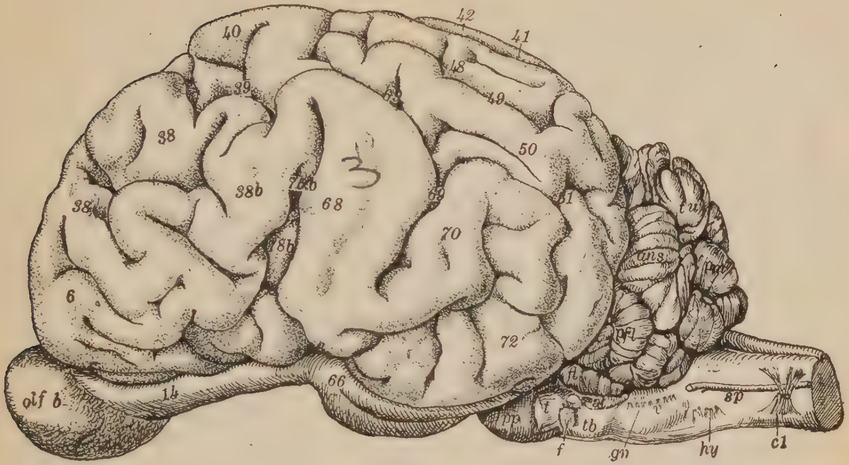

Fig. 18. Cerebrum of a cow, lateral view, × 1.

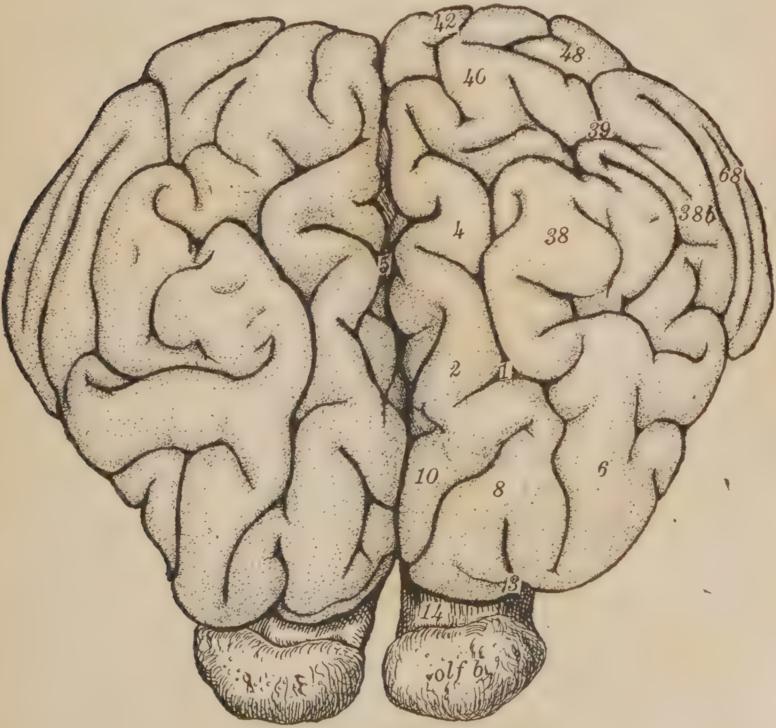

Fig. 19. Cerebrum of a cow, frontal view, × 1½.

represented by several partly united furrows. Its front end may be shallow or absent and here the gyri unite (48). Its posterior end may be joined by the **posterior lateral sulcus** (51) in the posterior border of the hemisphere.

The **lateral sulcus** (41) is a deep furrow on the dorsal surface that separates the **ectolateral gyrus** (52) from the **lateral gyrus** (42) that forms the dorsal border of the hemisphere as far back as the occipital pole. The **gyrus** (42) usually shows another shallow furrow in its thicker anterior part which may join the posterior part of the lateral sulcus as in the cat. The lateral sulcus (41) may be regarded as a sulcus limitans for the visual area. The anterior end of the lateral sulcus joins the **ansate sulcus** (39) or ends behind it. The **ansate sulcus** (39) in the dog is triradiate in form. The anterior limbs form the posterior boundary of the posterior sigmoid gyrus (4) while the posterior limb usually joins the lateral sulcus. In the dog it is quite evident that the ansate formation is a result of different developmental factors from those which produce the lateral sulcus (41).

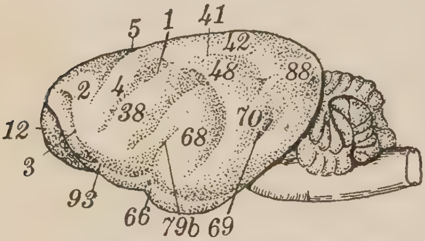

FIG. 20. Brain of a mink, lateral view, × 1¼.

Examine now the **medial surface** of the hemisphere (fig. 17). Three great systems of fibers unite the hemispheres and have been cut in making the median section. The **corpus callosum** (100) unites the cerebral cortex of one side with that of the other. The **anterior commissure** (99) in a like manner unites the olfactory bulbs and pyriform lobes (66). The **hippocampal commissure** (97) unites the hippocampal formations (104). Carefully remove the pia so that the sulci may be separated.

The pyriform area (66) and its dorsal continuation, the hippocampal gyrus (104) and the dentate gyrus, are ancient olfactory cortex (amphibian and reptilian). The **posterior rhinal fissure** (93) separates the temporal polar area from the pyriform area (66). Its upper end may be bifid, then the medial limb joins the calcarine sulcus (85). The lateral limb extends towards the lateral border which it sometimes crosses to unite with the posterior lateral sulcus (51).

The **calcarine sulcus** (85) (splenial) is a deep cleft of submerged cortex that separates the hippocampal gyrus (104) and the parasplenial gyrus (62) from the **lingual gyrus** (84) which forms the posterior occipital cortex. The upper end of the calcarine sulcus is continued forward as the **intercalary sulcus** (59) above the **parasplenial gyrus** (62) which it separates from the **suprasplenial gyrus** (90). Its anterior end cuts the dorsal border opposite the ansate sulcus where the medial border has been flexed. The **suprasplenial gyrus** (90) forms the medial surface of the dorsal border of the hemisphere, being the medial aspect of the lateral gyrus (42). It shows a shallow longitudinal cleft, the suprasplenial sulcus (89). The **lingual gyrus** (84) is an extensive cortex, cleft by a secondary furrow, the **postcalcarine sulcus** (85b). At its junction with the intercalary (59) the calcarine sulcus (85) often turns back towards the occipital pole and the occipital cortex presents an area folded around this end and circumscribed by the upper end of the postcalcarine sulcus (85b) as in figure 17.

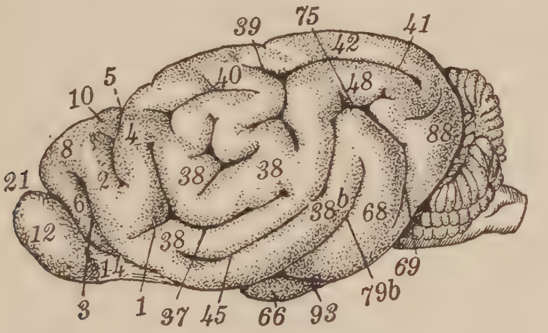

FIG. 21. Brain of a raccoon, lateral view, × 1.

The **crucial sulcus** (5) cuts the medial border well back of the anterior end of the corpus callosum (in the cat it is in front of it). This is accounted for by the greater development of the frontal cortex in the dog. The sulcus joins the intercalary and limits the **medial parietal gyrus** (56). In front of the sulcus is the **superior frontal gyrus** (10). The medial surface in front of the corpus callosum (100) is impressed with an irregular curved but shallow depression, the **genual sulcus** (31) which separates the frontal gyrus (10) from the ventrally situated **gyrus rectus** (22). The cortex in front of the anterior commissure and ventral to the corpus callosum is the **subcallosal gyrus** and **diagonal band** (32).

An interesting gyral pattern is seen in the Arctoid group of the Carnivora as represented by the brain of a mink (fig. 20), raccoon (fig. 21) and bear (fig. 22). In these brains the sylvian sulcus (79b) is well defined. The ectosylvian gyri (68 and 38b) in the bear are partly covered over by the suprasylvian arch (38 and 48). In the raccoon a similar condition is seen. In the mink the sulci are not fully differentiated. The suprasylvian gyri (38 and 48) are well developed as in other Carnivora in general. The posterior suprasylvian gyrus (50) is large in the bear. The lateral sulcus (41) is a deep cleft that surrounds the suprasylvian gyrus. In the bear its front end joins the coronal (1), but typically as in the raccoon it is independent of this sulcus. A short parietal sulcus (43) is seen in the bear.

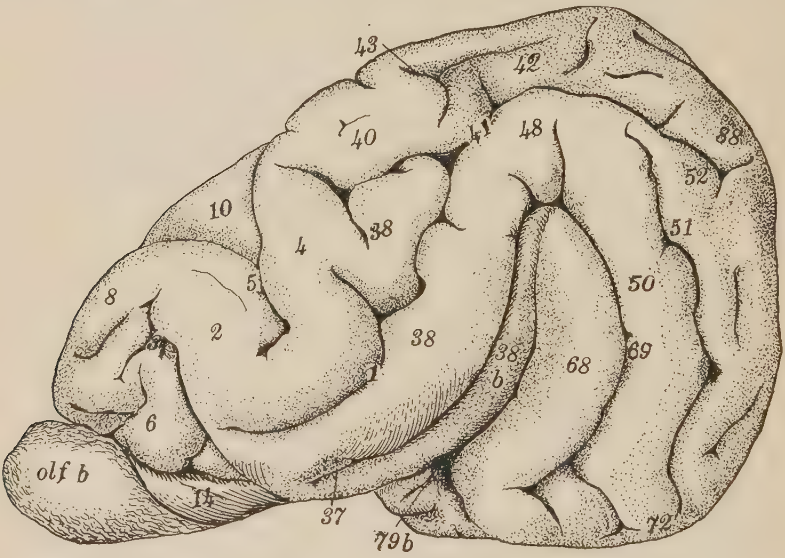

FIG. 22. Cerebrum of a bear, lateral view, × 1.

The sigmoid gyri (motor area) (2–4) which surround the crucial sulcus (5) are well developed. In the bear they have expanded and migrated ventrally on the surface; and the cortex of the superior frontal gyrus (10) appears on the dorsal surface (for the first time in Carnivora), as the ursine lozenge. Thus, in the bear, in which the capacity for prehension in the forelimbs and for erect posture in the hind limbs is fairly well developed, there is an expansion of the motor area and the crucial sulcus which takes on a marked resemblance to the superior precentral sulcus of the lower Primates.

The cortex behind the posterior sigmoid gyrus (4) and coronal sulcus (1) is well developed in the bear (38, 40) and very well in the arboreal raccoon (38, 40). In a related form, the small bear-like kinkajou (fig. 197), Brodmann has identified this region as the sensory area marked number 1. It appears that the great development in this region in the raccoon is due to the enlargement of the sensory area in connection with his arboreal mode of life. In the bear, the manual and prehensile functions of the forelimbs also demand a greater development of this important sensory area.

As a result of the great expansion of the motor and sensory areas in the raccoon and bear they give rise to an opercular formation that crowds forward over the deep presylvian sulcus (3) and downward so as to cover the anterior ectosylvian gyrus (38b) which in some members of this family is thus completely submerged in a sylvian fossa (75). Figure 24 of Lemur Fulvus makes an interesting comparison in this connection.

For the relation of the functional areas to the sulci and gyri see chapter 32.

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LIST OF NUMBERS FOR BRAINS OF CARNIVORA

1. Coronal sulcus
1b. Postcrucial sulcus
2. Anterior sigmoid gyrus
3. Presylvian (orbital) sulcus
4. Posterior sigmoid gyrus
5. Crucial sulcus
6. Inferior frontal gyrus
8. (Middle) frontal gyrus
10. Superior frontal gyrus
12. Olfactory bulb
13. Anterior limb of crucial sulcus
14. Olfactory stalk
21. Olfactory sulcus
22. Gyrus rectus
28. Cingular gyrus
29. Cingular sulcus
30. Parolfactory gyrus
31. Genual sulcus
32. Subcallosal gyrus and diagonal band
33. Rostral sulcus
34. Olfactory triangle
36. Olfactory tubercle
37. Anterior suprasylvian sulcus
38. Coronal gyrus (postcentral)
38b. Anterior ectosylvian gyrus
39. Ansate sulcus
40. Postcruciate gyrus
41. Lateral sulcus (intraparietal)
42. Lateral gyrus
43. Parietal sulcus
45. Diagonal sulcus
48. Middle suprasylvian gyrus
49. Ectolateral sulcus
50. Posterior suprasylvian gyrus
51. Posterior lateral sulcus
52. Ectolateral gyrus
53. Supracalcarine sulcus
59. Intercalary sulcus
62. Parasplenial gyrus
64. Insula
66. Pyriform area
68. Posterior ectosylvian gyrus
69. Postsylvian sulcus
70. Posterior suprasylvian gyrus
72. Inferior temporal gyrus
73. Inferior temporal sulcus
74. Temporal polar gyrus
75. Middle suprasylvian sulcus
75b. Anterior ectosylvian sulcus
75c. Circular sulcus
78. Posterior sylvian gyrus
78b. Anterior sylvian gyrus
79. Posterior ectosylvian sulcus
79b. Sylvian sulcus
80. Fusiform gyrus
82. Hippocampal fusiform gyrus
84. Lingual gyrus
85. Splenial or anterior calcarine sulcus
88. Posterior lateral gyrus
89. Suprasplenial sulcus
90. Suprasplenial gyrus
91. Amygdala
93. Rhinal sulcus
94. Uncus
95. Fornix
96. Dentate gyrus
97. Hippocampal commissure
98. Hippocampal rudiment
99. Anterior commissure
100. Corpus callosum
101. Thalamus
102. Septum pellucidum
103. Tuber cinereum
104. Hippocampal gyrus
105. Hippocampal fissure
106. Hippocampus
107. Optic tracts
109. Terminal lamina
110. Mammillary bodies
112. Nuclei septi

In the lists of numbers note that the odd numbers refer to sulci and the even numbers to gyri. In the two lists, as in the figures, the analogous structures have been given the same numbers, in order to facilitate comparison. The analogies are general and suggest a common origin. Close homologies are to be avoided because the processes of development of the cerebral pattens have diverged widely among the higher orders.

LIST OF NUMBERS FOR BRAINS OF PRIMATES

1. Central sulcus
2. Inferior precentral gyrus
3. Inferior precentral sulcus
4. Superior precentral gyrus
5. Superior precentral sulcus
6. Inferior frontal gyrus
7. Inferior frontal sulcus
8. Middle frontal gyrus
9. Superior frontal sulcus
10. Superior frontal gyrus
11. Diagonal sulcus
12. Olfactory bulb
13. Middle frontal sulcus
14. Olfactory stalk or peduncle
15. Fronto-orbital sulcus
16. Posterior orbital gyrus
17. Orbital sulcus
18. Lateral orbital gyrus
19. Frontal marginal sulcus
20. Medial orbital gyrus
21. Olfactory sulcus
22. Gyrus rectus
23. Ascending limb of sylvian sulcus
24. Subcentral gyrus
25. Horizontal limb of sylvian sulcus
26. Paracentral gyrus
27. Posterior cingular sulcus
28. Cingular gyrus
29. Anterior cingular sulcus
30. Parolfactory gyrus
31. Genual sulcus
32. Subcallosal gyrus and diagonal band
33. Rostral sulcus
34. Olfactory triangle
35. Medial precentral sulcus
36. Olfactory tubercle
37. Inferior postcentral sulcus
38. Inferior postcentral gyrus
39. Superior postcentral sulcus
40. Superior postcentral gyrus
41. Intraparietal sulcus
42. Anterior superior parietal gyrus
43. Superior parietal sulcus
44. Posterior superior parietal gyrus
45. Transverse postcentral sulcus
46. Anterior marginal gyrus
47. Marginal sulcus
48. Posterior marginal gyrus
49. Angular sulcus
50. Angular gyrus
51. Anterior occipital sulcus
52. Parieto-occipital gyrus
53. Transverse occipital sulcus
54. Paroccipital gyrus
55. Paroccipital sulcus
56. Anterior precuneal gyrus
57. Parietal marginal sulcus
58. Posterior precuneal gyrus
59. Parieto occipital sulcus
60. Anterior perforated substance
61. Precuneal sulcus
62. Parasplenial gyrus
63. Subparietal sulcus
64. Insula
65. Simian sulcus (Affenspalte)
66. Pyriform area
67. Transverse occipital sulcus
68. Superior temporal gyrus
69. Superior temporal sulcus
70. Middle temporal gyrus
71. Middle temporal sulcus
72. Inferior temporal gyrus
73. Inferior temporal sulcus
74. Temporal polar gyrus
75. Sylvian fissure
76. Occipito-temporal gyrus
77. Inferior occipital sulcus
78. Transverse temporal gyrus

79b. Transverse temporal sulcus

80. Fusiform gyrus
81. Transverse collateral sulcus
82. Hippocampo-fusiform gyrus
83. Collateral sulcus
84. Lingual gyrus
85. Calcarine fissure
86. Superior occipital gyrus
87. Lateral occipital sulcus
88. Inferior occipital gyrus
89. Cuneal sulcus
90. Cuneal gyrus
91. Amygdala
92. Occipital polar gyrus
93. Posterior rhinal sulcus
94. Uncus
95. Fornix
96. Dentate gyrus
97. Hippocampal commissure
98. Hippocampal rudiment
99. Anterior commissure
100. Corpus callosum
101. Thalamus

CHAPTER 4

THE FRONTAL LOBE OF PRIMATES

So important is the knowledge of the cerebral cortex to the biologist, physiologist and student of animal and human behavior that the evolution of the cerebral pattern of the Primates will be briefly sketched, and certain analogies with the brains of the Carnivora will be indicated.

In lemurs, monkeys, apes and man (Primates) the cerebral cortex is greatly developed. Thus there is a great increase in the complexity of the cerebral pattern in the occipital, temporal and parietal regions. But the most remarkable feature of Primate brains is the development of the large frontal lobe. In the Carnivora, such as the dog and cat, the coronal sulcus and the small postcrucial depression may be taken as homologues of the central sulcus of Rolando of the primate order. These may be regarded as very fundamental sulci that form a natural boundary between the motor cortical area in front and the area of deep sensibility behind them. Such are spoken of as limiting sulci. For this study the fissural patterns of the brains of the Cebidae (New World monkeys), the Cercopithecidae (Old World monkeys), the Simidae (higher anthropoid apes) will be demonstrated and compared with the cerebral pattern of a human fetus and a newborn babe.

In dealing with the cortex of the Carnivora (and the Ungulata may be included) it has been stated that all the cortex in front of the coronal and the postcrucial sulci constitutes the frontal lobe.[1] This comprises the crucial, frontal and orbital gyri and the anterior end of the opercular sulcus. It is noteworthy that in the Carnivora this frontal lobe is small in size and is dominated by the crucial formation and the crowding forward of the opercular formation which gives rise to the deep presylvian sulcus. This is to be correlated with the lowly developed voluntary motor functions of these animals.

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[1] The anterior olfactory and precommissural areas are not included in this consideration.

In the Primates all the cortex in front of the central sulcus (coronal) constitutes the frontal lobe. This includes the precentral, frontal and orbital cortex which has so greatly expanded along new lines and replaces the presylvian and crucial formation of the Carnivora. This great frontal area has displaced the whole opercular formation downwards and backwards over the insula. The great size of the frontal cortex in the Primates is at once evident and the formation of a complex series of new sulci and gyri can readily be traced from lemurs to monkeys, apes and man. This is correlated with the evolution of the great prehensile function of the forelimb, walking and prehensile function of the hind limb; and finally in man the functions of the articulate speech. The muscular movements and composite motor reactions of monkeys and especially man are no longer simple reactions of walking, feeding, etc., but are capable of innumerable variations. The thousands of special adaptative movements to which the hand and body of man may be trained is in no small measure dependent upon the great development of the frontal lobe.

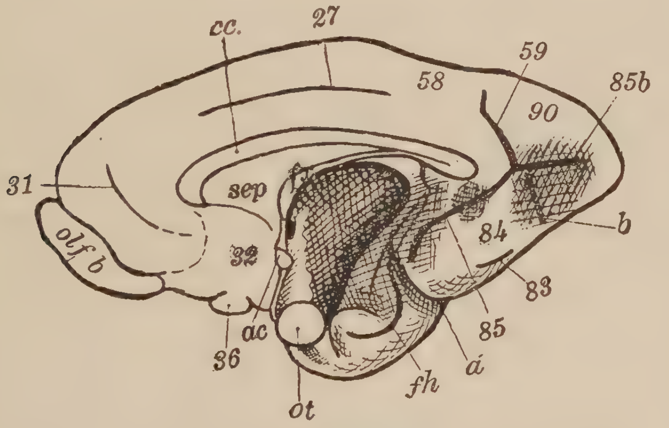

Fig. 23. Cerebrum of lemur fulvus, medial view of right half. From G. E. Smith.

The frontal lobe of Cebidae, figures 25 to 28

The frontal lobe of the New World monkeys is large, constituting the frontal third of the hemisphere. It presents three surfaces, an orbital, a lateral and a medial. The brains of cebus and lagothrix are shown in the figures. For explanations of numbers see page 27.

The **orbital surface** (20) is wide and concave and overlies the bony orbit. It is inclined upwards and its medial border overlies a reduced olfactory bulb (12) and stalk (14). The olfactory stalk lies in a shallow groove, the olfactory sulcus, medial to which is the gyrus rectus (22) forming the medial border. A shallow *Y*-shaped or straight **orbital** sulcus (17) appears in the middle of this surface dividing it into a medial, a lateral and a posterior orbital gyrus. The latter is included between the two posteriorly directed limbs of the sulcus. A fronto-orbital sulcus (15) appears under the inferior frontal gyrus (6), well seen in lagothrix. In cebus it is combined with the orbital.

The **lateral surface** is broad and convex. In front it joins the orbital surface at the orbital margin which is undercut by the fronto-orbital sulcus (15). Over the dorsal margin it joins the medial surface. Posteriorly it is limited by a deep cleft, the **central sulcus** (1) of Rolando which is comparable to the coronal sulcus of Carnivora. This is short and straight in cebus but longer and bent in lagothrix. The cortex in front of this is the **precentral gyrus** (2–4), and constitutes the **motor area.** In front of this and placed near the lower level is a curved *T*-shaped furrow, the **inferior precentral sulcus** (3). Its vertical limb is long in cebus. In front of this and above the orbital margin is a horizontal furrow, the inferior **frontal sulcus** (7) (*s. rectus*) which extends almost to the frontal pole and separates the inferior from the middle frontal gyrus. In lagothrix it is combined with the precentral. The ventral margin of the frontal lobe is formed by an **opercular formation** (2) comparable to that of the Carnivora. This, in the Primates, is shifted backwards so that it conceals the insula and comes in apposition with the superior temporal gyrus (68) forming thus a new cleft, the **sylvian fissure** (75) of the Primates. When the lips of this fissure are separated the **insular cortex** is exposed and the deep **circular sulcus** is seen separating the opercular formation from the insula. The anterior end of the operculum curves medially to join the orbital area in front of the insula so that this end of the sulcus is scarcely seen from the orbital side. There are small depressions that form the superior precentral (5) and superior frontal sulci (9); otherwise the superior and middle frontal gyri (10, 8) still form a common cortical area.

The medial surface (figs. 26–28) consists of the part dorsal to and the part in front of the corpus callosum (100). The cortex dorsal to the corpus callosum is divided by a long horizontal furrow, the **cingular sulcus** (27, 29) into a ventral area, the **cingular gyrus** (28), which borders the corpus callosum and a dorsal area, the medial surface of the **superior frontal gyrus** (10), and the paracentral gyrus (26). The cortex in front of the corpus callosum is cleft by a shallow **genual sulcus,** or a compensating rostral sulcus (33). Below the latter forming the ventral margin is the gyrus rectus (22).

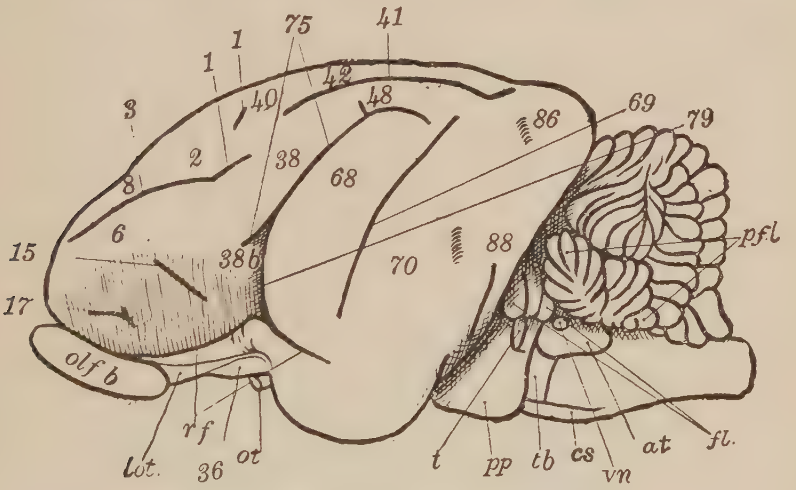

Fig. 24. Brain of lemur fulvus, lateral view. From G. E. Smith.

The frontal lobe of the baboon (cynocephalus), figures 29, 30

This monkey has a doglike muzzle and on this account the brain case is more elongated than that of the Cebidae, which influences the shape of the brain. The frontal lobe is relatively smaller, more compressed dorso-ventrally, but presents a similar though more elaborate pattern of gyri and sulci.

The orbital surface is deeply concave. It is cleft by two or **three orbital sulci.** The medial one (17) borders the **gyrus rectus** (22), the lateral one or fronto-orbital sulcus (15) extends to the middle of the orbital margin and its posterior end divides in front of the insular margin of this surface.

The lateral surface is convex. The **central sulcus** (1) is longer than in cebus extending slightly over the medial border of the hemisphere. Its lower end is curved but does not reach the sylvian fissure (75). Here it is replaced by a short diagonal sulcus (11) which in the higher apes joins the lower end of the inferior precentral sulcus.

The **inferior precentral sulcus** (3) is a strongly developed *T*-shaped furrow. Its vertical limb forms the front boundary of the **inferior precentral gyrus** (2) which it separates from the **inferior frontal gyrus** (6). Its horizontal limb separates the **middle frontal gyrus** (8) into two parts. Above the orbital margin is a horizontal furrow, the **inferior frontal sulcus** (7) which separates the inferior frontal gyrus (6) from the anterior end of the middle frontal gyrus (8).

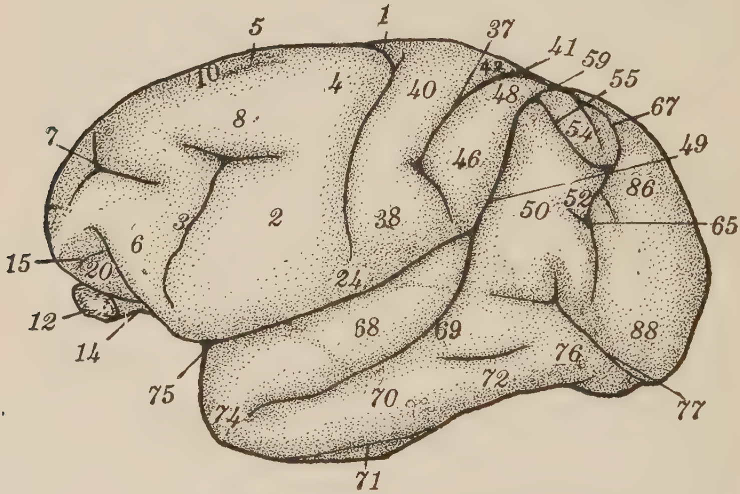

FIG. 25. Cerebrum of cebus capucinus, lateral view, × 1½.
For explanation of numbers see page 27.

Dorsal to its anterior end is another sulcus that cuts across the superior frontal gyrus and may join the inferior frontal sulcus to form a *Y*-shaped furrow. The **superior frontal gyrus** (10) is the cortex along the medial border. Two or more shallow dorsally placed depressions constitute the middle frontal sulcus (13). The most posterior one separates the gyrus (10) from the middle frontal gyrus (8), both of which are directly continuous with the **superior precentral gyrus** (4). The separation of these gyri is feebly realized but the anthropoid characteristics are clearly indicated. In the **opercular formation** (24) short subcentral sulci are seen in front and back of the lower end of the diagonal sulcus (11). The front end of the operculum turns medially to join the posterior border of the orbital surface. The opercular formation conceals the insula.

This is poorly developed so that the circular sulcus is not seen on the surface.

The medial surface above the corpus callosum (100) is cleft by a long **cingular sulcus** (29). The posterior part (27) of this separates the paracentral gyrus (26) formed by the medial surfaces of the **precentral** and **postcentral gyri** from the **cingular gyrus** (28) which borders the corpus callosum (100). This end of the sulcus turns up to cut the dorsal border of the hemisphere behind the postcentral gyrus (26). This is another anthropoid feature. The anterior part of the sulcus separates the medial surface of the frontal gyrus (10) from the cingular gyrus (28). The cortex in front of the corpus callosum is cleft by a shallow **genual sulcus** (31) that splits and radiates towards the frontal pole. Below this is a small **rostral sulcus** (33).

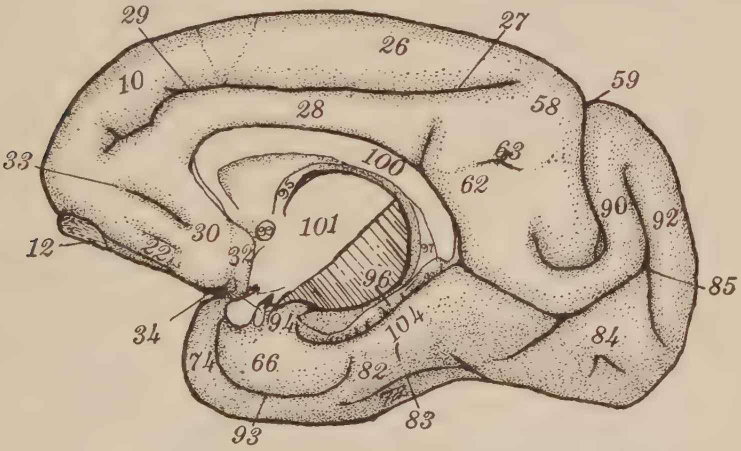

FIG. 26. Cerebrum of cebus capucinus, medial view of right half, × 1½.

The frontal lobe of a seven month human fetus, figures 31–34

The cortex of the human fetus in the seventh month presents a cerebral pattern resembling that of the lower apes. The frontal lobe is large, forming about two-fifths of the hemisphere. A deep **central sulcus** (1) forms its posterior boundary. This nearly cuts the dorsal medial border where the **precentral** (4) and the **postcentral gyri** (38, 40) unite around its end. This union forms the paracentral gyrus (26) and is bounded on the medial side by the **posterior cingular sulcus.** The **superior frontal cortex** (10) is broad and indented by a series of three shallow depressions as in the lower monkeys.

On the right side the confluence of these into a single superior frontal sulcus (9) is already in progress so that this cortex is divisible into a **superior** (10) and **middle frontal gyrus** (8). The cortex of the superior one passes over onto the medial surface where it is bounded by the **anterior cingular sulcus** which separates it from the **cingular gyrus.** The posterior depression of the superior frontal sulcus may be regarded as the **superior precentral sulcus** (5). Thus the **superior precentral gyrus** (4) is already well defined. It should be noted that both the superior and middle frontal gyri join the precentral as in the apes. The **inferior precentral sulcus** (3) is a *T*-shaped furrow as in the apes. The vertical limb separates the **inferior precentral gyrus** (2) from the **inferior frontal gyrus** (6). These are continuous around its ventral end along the operculum. The horizontal limb separates the **middle frontal gyrus** (8) from the **inferior frontal gyrus** (6). In front of and below this limb there is a small depression, the beginning of the **inferior frontal sulcus** (7). It is noteworthy that the cortex of the frontal pole in the human brain is greatly developed as compared with the apes. The **opercular formation** (24) partially conceals the insula (64). In the human fetus and to less extent in the anthropoid apes, an orbital operculum (16) is formed around the front part of the insula due to the additional growth and crowding of the cortex in this region. This crowding gives rise to the **anterior ascending ramus** (23) and the **horizontal ramus** (25) of the sylvian fissure.

The orbital surface (fig. 34) is expanded laterally so that the frontal operculum (16) has a more lateral direction. In front of it is the **fronto-orbital sulcus** (15) and medial to this is the **orbital gyrus** (18), both vaguely indicated and more or less confluent. The olfactory bulb (12) and tract lie in the **olfactory sulcus** (21).

The frontal lobe of anthropoid apes and man

The smallest of the anthropoid apes is the gibbon. Compare its frontal lobes (figs. 41, 42) with those of the baboon and human fetus. An inferior frontal sulcus (*sulc. rect.*) joins a small inferior precentral sulcus (3). A superior frontal sulcus (*sulc. sup. front.*) occurs in the dorsal region. The central sulcus (*sulc. cent.*) is well defined.

The fissural pattern of the frontal lobe of the anthropoid apes (figures — gorilla 35–36, orang 37–38 and chimpanzee 39–40) has attained a degree of marked stability. The sulci and gyri are to be compared with those of the human fetus (figs. 31 to 34) and those of a newborn babe (figs. 43, 44).

The central sulcus (1) is a deep sinuous cleft which cuts the lateral surface from the dorsomedial margin to the middle of the opercular formation (24). Around each end of it the **precentral gyrus** (2, 4) is continuous with the postcentral gyrus (38, 40). On the medial surface this union is limited by the posterior cingular sulcus (27) and on the opercular margin by the **subcentral sulcus.** In the human brain there is a marked elongation of the **superior precentral gyrus** (4) so that its connection with the **middle frontal gyrus** (8) is carried to a lower level. In the human babe the upper end is often bordered by a deep **medial precentral sulcus** (35) scarcely apparent in the apes though usually present as a slight cleft in the mesial border. Its appearance in the human fetus suggests a false analogy to the crucial sulcus of the Carnivora, though its late origin as a sulcus limiting the precentral gyrus is evident. In the superior precentral region there is a deep triradiate furrow whose vertical limb, the **superior precentral sulcus** (5) borders the front of the precentral gyrus (4), and whose horizontal limb, the **superior frontal sulcus** (9), often short, separates the **superior frontal gyrus** (10) from the **middle frontal gyrus** (8) and may or may not join the larger **middle frontal sulcus** (13) in front of it. When the union does not occur as is usual in the apes, the superior and middle frontal gyri unite in front. In all cases they pass back around the precentral sulcus (5) and join the precentral gyrus (2). In the apes the **middle frontal sulcus** (13) is a short curved and often irregular furrow over whose downcurved posterior end the middle frontal gyrus (8) splits to join the superior one (10). This feature is constant in the apes and usual in the babe. In the apes the front end of the **superior frontal gyrus** (10) is quite narrow and a depression or two may appear in its surface. In the human brain this gyrus is often highly developed and the furrows in it, by joining with the superior frontal sulcus make the superior frontal sulcus (9) appear quite long and medial to and independent of the middle frontal sulcus. In this way the frontal region may present four frontal gyri and three sulci, a superior, a middle and an inferior one. The middle frontal sulcus (13) is often called the superior frontal by other authors.

The **inferior precentral gyrus** (2) is bounded in front by a *Y*-shaped sulcus. This **inferior precentral sulcus** (3) becomes a very complex and radiating sulcus in the large apes and man. The vertical limbs are the **inferior precentral sulcus** (3) and its upper horizontal limb is directed forward separating the posterior end of the **inferior frontal gyrus** (6) from that of the **middle frontal gyrus** (8). It often joins the **inferior frontal sulcus** (7) in front of which it separates the front ends of these gyri. The **inferior frontal sulcus** (7) in the apes is often bifid at its front end but the upper limb is to be classed as a part of the superior frontal formation. In the human brain the gyri have greatly expanded and are more convoluted; the middle (8) often forming a thick irregular lobule and the lower one forming the **frontal operculum** (6). The **circular sulcus** separates this from the insula. In the apes the **orbital** (16) and **frontal opercula** (6) are meagerly developed and a deep **fronto-orbital sulcus** (15) cleaves the orbital border in front of them. Cunningham believed that the orbital operculum of apes becomes the anterior part of the insula in man and that the fronto-orbital sulcus of apes is homologous with the orbital opercular sulcus. The conditions in the brains of the chimpanzee and gorilla suggest this as a possible interpretation. But the brain of the orang which is more comparable with the human in this and in several other respects shows that the orbital operculum is developed behind a **fronto-orbital sulcus** (15), a condition which can also be recognized in the human brain. Above the orbital margin the superior and middle frontal gyri are limited in the human brain by a new **fronto-marginal sulcus** (19) seldom found in the apes where this position is usually taken by the front end of the similar looking inferior frontal sulcus (7). Likewise the sulcus radiatus (19b) is added in well-developed human brains due to the enlargement of the orbitomarginal area that surrounds it. The frontal operculum (6) is simple in the apes and here, as in the human, an **ascending ramus** (23) of the sylvian fissure is recognized. In the human brain the operculum is greatly developed and convoluted. The gyrus just behind the ascending ramus is usually depressed or infolded over the **diagonal sulcus** (11) and a **horizontal ramus** (25) appears between the frontal and orbital opercula.

The orbital surface is concave and cleft in the middle by an irregular orbital sulcus (17) which separates the **lateral orbital** (18) from the **medial orbital gyrus** (20). The **olfactory sulcus** is found dorsal to the olfactory bulb (12) and stalk. Medial to it is the gyrus rectus (22). In the apes the deep **fronto-orbital sulcus** (15) cuts the lateral surface and bounds the orbital operculum. In the orang and human brains this sulcus (15) has a different and more forward position due to the forward crowding of the inferior frontal gyrus (6).

The **medial surface,** dorsal to the corpus callosum (100), is cleft by the deep **cingular sulcus** (29). Its posterior part (27) separates the **cingular gyrus** (28) from the **paracentral gyrus** (26) which is a cortical area that unites the medial ends of the precentral (4) and postcentral (40) gyri. In the human a **medial precentral sulcus** (35) is often seen in front of the medial end of the precentral gyrus. The front end of the cingular sulcus (29) separates the cingular gyrus (28) from the medial surface of the superior frontal gyrus (10). The latter is pitted by a number of irregular furrows (paracingular sulcus). The cortex in front of the corpus callosum is cut by a **genual sulcus** (31) which may join the cingular or cut the anterior margin of the hemisphere. At a lower level is another variable **rostral sulcus** (33) that tends to border or radiate towards the frontal pole. Below the rostrum of the corpus callosum is seen the small **subcallosal gyrus** (32) and in front of it are the **parolfactory gyrus** (30) and the **gyrus rectus** (22).

The **origin of the frontal lobes** and their great size in Primates is not due to any direct sensory connection as is that of the parietal, temporal, occipital and olfactory lobes. Biologically they appear to be an outgrowth of the motor (precentral) areas much as the socalled association areas are outgrowths of the sensory areas. The lower Primates were vociferous, freely moving, arboreal animals with prehensile limbs and reduced olfactory organs and muzzle. Their mode of life called for a vastly greater accuracy and refinement in limb movements than is necessary in the quadrupeds. In the cerebrum this first expressed itself in the great development of the sensomotor areas, for the awareness of position and guiding of movements. In addition the visual and auditory areas, the chief analysers of the external environment, became the assistants of the sensomotor areas in directing the movements of the animal. This assistance was achieved through subcortical fiber connections with the frontally located motor areas. These have in consequence induced the growth of the frontal cortex. With refinement and specialization of the motor functions the frontal lobes have attained a large size in Anthropoids and a truly extraordinary size in Man in whom associational processes have reached a higher level.

CHAPTER 5

The Parietal Lobe of Primates

In the Carnivora the parietal lobe has been defined as including the dorsolateral cortex back of the coronal sulcus and above the sylvian and anterior rhinal sulci. It thus comprises the cortex of the coronal, anterior sylvian and ectosylvian, middle ectosylvian and suprasylvian and lateral gyri and the corresponding sulci.

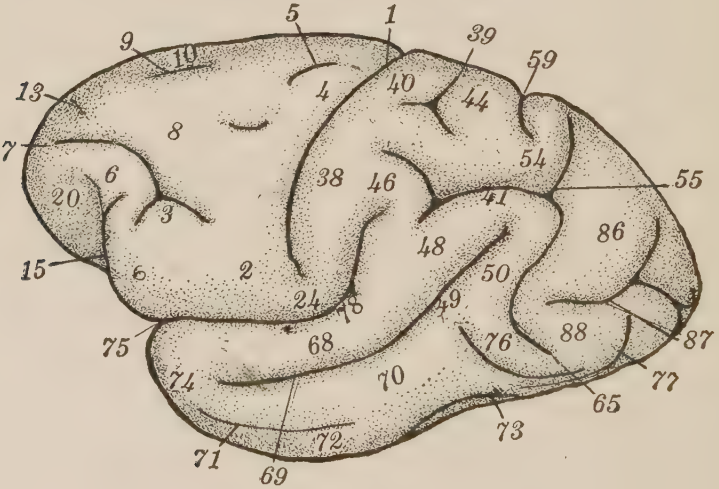

Fig. 27. Cerebrum of lagothrix, lateral view, × 1½.

In the Primates the parietal lobe comprises the cortex posterior to the central sulcus (1) and dorsal to the sylvian fissure (75). The **paroccipital sulcus** at the bottom of the Affenspalte (65) and the anterior lip of this cleft may be taken at its posterior limit. It includes the cortex of the postcentral, superior and middle parietal, marginal and angular gyri and the corresponding sulci. On the medial surface it includes the precuneal gyrus, the posterior part of the paracentral gyrus and the splenial gyrus. For numbers see page 27.

The parietal lobe of Cebidae, figures 25 to 28

The brain of these New World monkeys is instructive because it presents the simian cerebral pattern in a very simple form. The small size of these animals and the general oval shape of their brain case should be kept in mind. The parietal lobe is limited in front by the central sulcus (1), below by the sylvian fissure (75) and posteriorly by the transverse occipital sulcus (65, Affenspalte of higher Simidae). On the medial surface it includes the precuneal gyrus (58) bounded in front by the upturned end of the cingular sulcus (27) and behind by the parieto-occipital fissure (59). A comparison with higher apes and man shows the relative low development of superior parietal and precuneal gyri in the Cebidae. The Affenspalte (65) is a superficial sulcus so that none of the parieto-occipital gyri and sulci are covered over by an operculum as in the baboons and higher apes.

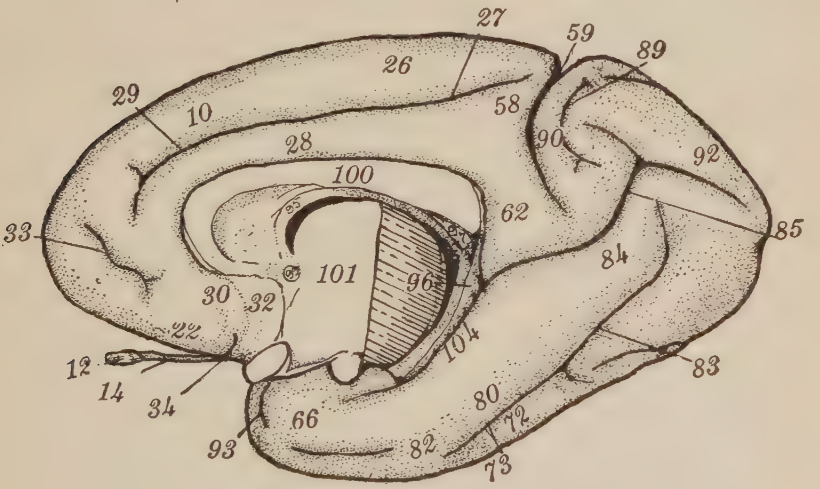

FIG. 28. Cerebrum of lagothrix, medial view of right half, × 1½.

The **postcentral gyrus** (38–40) is bounded in front by the **central sulcus** (1) and behind by the **inferior postcentral sulcus** (37) which in these monkeys is only the anterior end of the intraparietal sulcus. The dorsal half of the postcentral gyrus (40) is fused with the small **superior parietal gyrus** (44). In lagothrix a superior postcentral sulcus (39) is present. The ventral half of the postcentral gyrus (38) joins the anterior limb of the **marginal** (46) and **precentral** (2) gyri to form the operculum.

The **superior parietal gyrus** (42) is small as compared with that of apes and man. It is limited behind by the **parieto-occipital fissure** (59), below by the **intraparietal sulcus** (41) and in front it is fused with the upper end of the postcentral gyrus (40). In lagothrix the superior postcentral sulcus (39) indicates a partial separation from the postcentral gyrus.

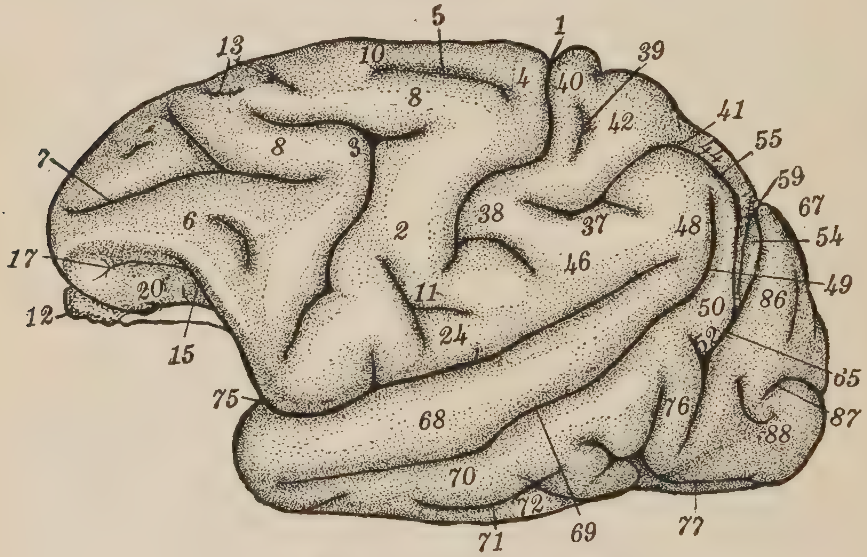

Fig. 29. Cerebrum of baboon, lateral view, × 1½.

The **precuneal gyrus** (58) on the medial surface joins the superior parietal gyrus over the medial margin of the hemisphere. In cebus a small depression, the **subparietal sulcus** (63) separates it from the parasplenial gyrus (62). As this sulcus depends on the growth of several surrounding areas it may vary greatly and be replaced by other neighboring sulci.

The **inferior parietal gyrus** is formed of the **marginal** (46–48) and **angular** (50) **gyri.** The marginal gyrus is included between the sylvian fissure (75) and intraparietal sulcus (41) and forms the parietal operculum. It is a most straight as compared with the curved *T*-shaped convolution of apes and man and joins the superior temporal gyrus over the end of the sylvian fissure. The union is seen in lagothrix but is deeply submerged in cebus. The Cebidae have a prehensile tail, but their most variable feature is the development and use of the thumb. Cebus has a poorly developed thumb. In lagothrix it is well developed. The **angular sulcus** (49) is confluent with the joined upper ends of the superior temporal (69) and sylvian sulci. It separates the marginal (48) from the **angular gyrus** (50) except above its upper end where they are united. The angular gyrus (50) is narrow above and broadens out below to join the middle temporal gyrus. Though small in lagothrix it is large in cebus. In another species, ateles, it is joined to a small but distinct parieto-occipital gyrus (52). Posteriorly the angular gyrus appears to be bounded by the **transverse occipital sulcus** (67) or Affenspalte (65). The parieto-occipital sulcus (59) is surrounded by the paroccipital gyrus (54) which may be considered as an annex of the superior parietal gyrus (44) in lagothrix. In cebus an analogous gyrus is joined with the upper end of the angular. Thus on the surface in cebus the angular gyrus (50) is in some specimens continued back into the cortex in front of the Affenspalte, or transverse occipital sulcus. The paroccipital gyrus (54) of Cebidae is the forerunner of the **paroccipital gyrus** of higher forms.

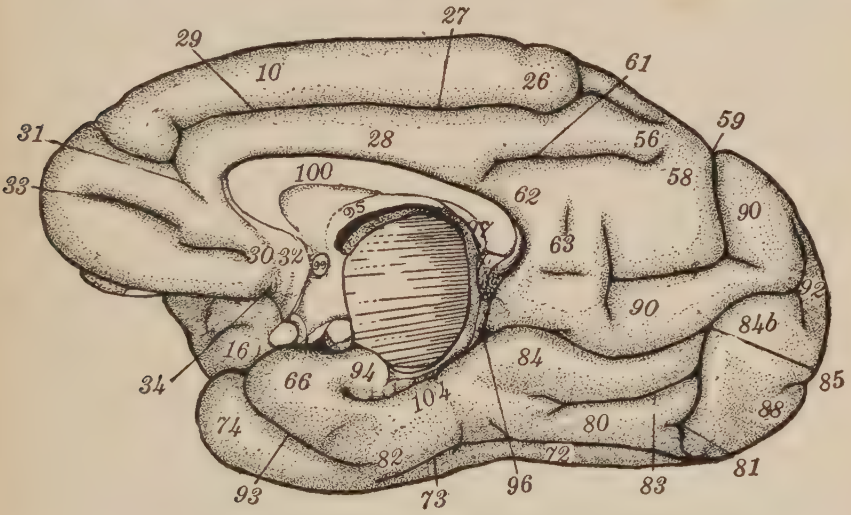

FIG. 30. Cerebrum of baboon, medial view of right half, × 1½.

The parietal lobe of the baboon, figures 29, 30

The parietal lobe of the baboon is small as compared with that of apes and man. It is bounded in front by the **central sulcus** (1), posteriorly by the **transverse occipital fissure** (Affenspalte) and below by the **lateral fissure** (sylvian). A comparison of the figures will show how this area, small in the baboon, gradually increases in the chimpanzee, gorilla, and orang to man. The **postcentral gyrus** (38) is narrow below and bent around the front end of the **inferior postcentral sulcus** (37) to join the **parietal operculum** (46, 48). The upper end of the gyrus merges with the superior parietal gyrus but a small depression, the **superior postcentral sulcus** (39), indicates a partial separation. On the medial surface the posterior end of the **cingular sulcus** (27) cuts the medial margin just behind the postcentral gyrus and further indicates its separation from the superior parietal gyrus.

The superior parietal gyrus is very small. The superior postcentral sulcus (39) indicates a separation into two gyri, a condition fully realized in apes and man. Its medial surface (fig. 30) is depressed by the posterior end of the **cingular sulcus** (27) and forms the **precuneal gyrus** (56). A straight **precuneal sulcus** (63) separates this from the **parasplenial gyrus** (62). The posterior ends of the superior parietal and precuneal cortex sink into the **parieto-occipital fissure** (59) and join the **paroccipital gyrus** (54) which surrounds the upper end of this fissure.

The **intraparietal sulcus** (41) is a deep cleft that separates the superior parietal gyrus (44) from the **angular** (50) and **marginal** (48) gyri which together constitute the **inferior parietal gyrus** or suprasylvian formation. The anterior end of this sulcus is confluent with the inferior postcentral, a condition usually seen in apes and man. Its posterior end joins the paroccipital sulcus which in turn descends as the **transverse occipital sulcus** (65) or Affenspalte. In its relation to the postcentral, superior parietal, marginal, angular and paroccipital gyri, the intraparietal sulcus presents a remarkable analogy to the lateral sulcus of Carnivora.

The **marginal gyrus** (48) joins with the postcentral (46) to form the **parietal operculum.** The marginal gyrus is poorly developed in the baboon as compared to that in apes and man. In all Primates it unites with the **superior temporal gyrus** (68) over the posterior end of the **sylvian fissure** (75). This end is straight in the lower simia but upturned in apes and man. Back of this union the **angular sulcus** (49) separates the **angular gyrus** (50) from the marginal which unite over its dorsal end. The lower end of the angular sulcus is continued into the superior temporal sulcus (69). A comparison of the figures will show that this *T*-shaped union of the marginal and angular formation is a constant feature in the brains of the Primates. Posteriorly the angular gyrus (50) is bounded by the paroccipital sulcus and lower end of the Affenspalte (65). The marginal gyrus may be compared with the conjoined anterior suprasylvian and posterior ectosylvian gyri of Carnivora if we suppose the anterior sylvian and ectosylvian have been absorbed in the under surface of the parietal operculum. A reduced muzzle in the Primates also favors this view. There is no direct evidence of this change in the simian brains although in the higher Carnivora, as for example the bear (fig. 22) and the lemur (fig. 24), such a transformation is indicated (see pages 24 and 59).

The parietal lobe of a seven-month human fetus, figures 31–33

The parietal lobe of a seven-month human fetus shows some characteristic features of the cerebral cortex of Primates. The lobe is bounded in front by the central sulcus (1), below by the sylvian fissure (75) and posteriorly by the paroccipital sulcus (55) and the anterior occipital sulcus comparable to the anterior lip of the simian sulcus of apes. A series of sulci, the inferior postcentral, intraparietal and the paroccipital separate it into the superior and inferior parietal and postcentral gyri. On the medial surface it includes the precuneal gyrus.

The postcentral gyrus (38–40) is well defined by the confluent **postcentral sulci** (37–39) on the right side. On the left side the superior postcentral sulcus is not formed. Certain curves and enlargements are already evident in the gyrus which are forerunners of the adult conditions. The lower end of the postcentral gyrus unites with the marginal and precentral gyri to form the operculum (24). Here the small **subcentral sulci** are appearing. The upper end is in like manner united along the medial margin with the precentral (26) and superior parietal gyri (42). On the medial surface this union is marked off by the **posterior cingular sulcus** (27).

The **superior parietal gyrus** (42) is a large simple convolution continuous over the medial border with the precuneal gyrus. A **precuneal sulcus** appears in the surface of the latter and the parieto-occipital sulcus (59) forms its posterior limit. Anteriorly the superior parietal gyrus joins the postcentral, but on the right side a definite postcentral sulcus partly separates them. A shallow furrow over the medial border indicates the marginal parietal sulcus which at a later date separates this gyrus into an anterior and posterior part. A true superior parietal sulcus is not evident. The superior parietal gyrus shows a strong resemblance to that of the simian brain.

The **intraparietal sulcus** (41) is well formed and its independence of the inferior postcentral (37), paroccipital (55), and anterior occipital (51) is clearly evident. A disruption of this continuity is characteristic of human brains. On the right its form is often radiate and may consist of two parts, one above the marginal and another above the angular gyrus. Its form appears to be influenced by the precocious growth of these gyri. Most often it is disconnected from the paroccipital.

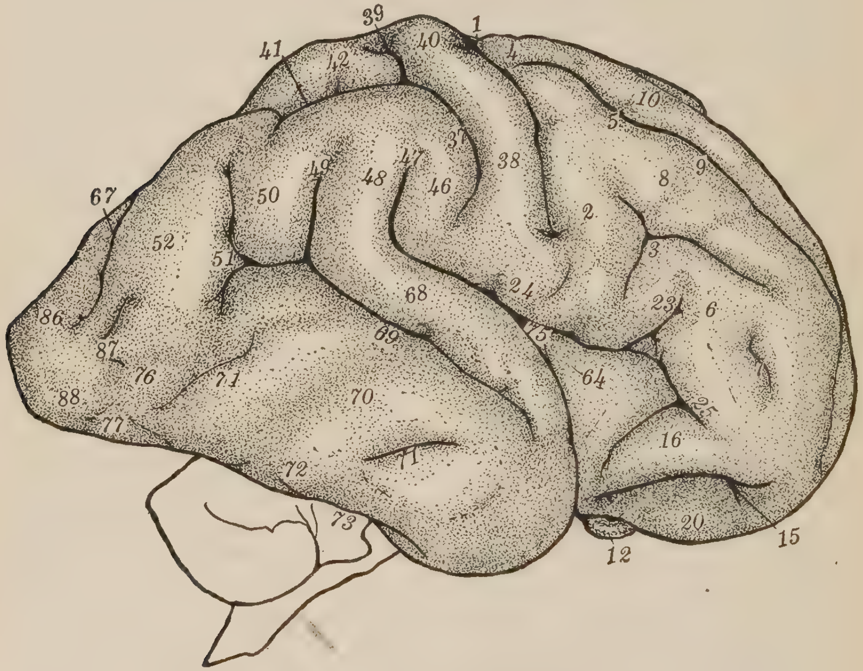

FIG. 31. Cerebrum of a seven-month human fetus, right view, ×1¼. For explanation of numbers see page 27

The **inferior parietal lobule** is a *T*-shaped convolution formed by the union of the marginal (48), angular (50), and the parieto-occipital (52) gyri. The marginal gyrus (48) joins with the superior temporal (68) and thus forms the stem between the upturned end of the sylvian fissure (marginal sulcus) and the **angular sulcus** (49). Around the former it turns forward and joins the postcentral gyrus to form the parietal operculum. When this is raised a transverse (anterior sylvian) gyrus is seen on the under surface. The **angular gyrus** (50) is a continuation of the marginal over the upper end of the angular sulcus, well seen on the right side. The lower end is cut off from the middle temporal gyrus but a union is usually evident here, such as is found in the apes. The **anterior occipital sulcus** (51) separates the angular gyrus from the **parieto-occipital gyrus** (52).

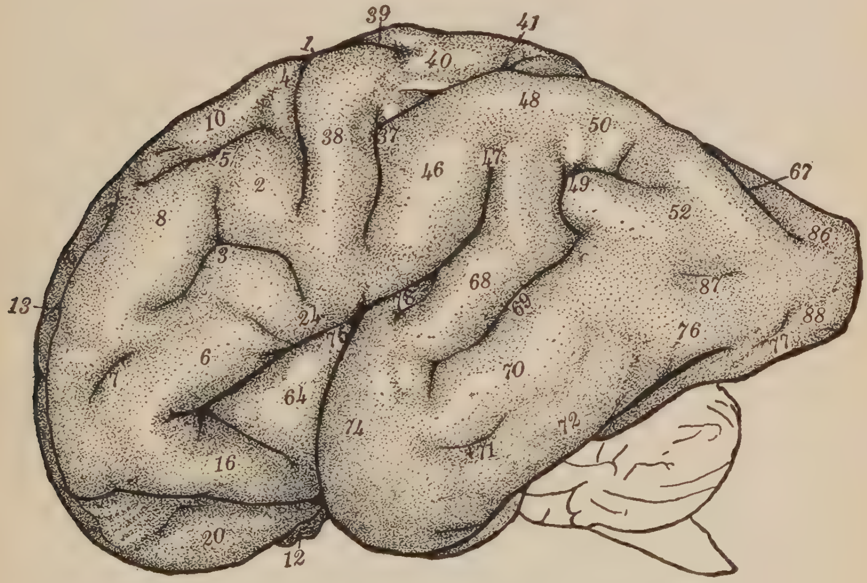

FIG. 32. Cerebrum of a seven-month human fetus, left view, × 1¼.

Over the upper end of the sulcus this gyrus usually unites with the angular, though it may also be joined with the superior parietal gyrus around the incomplete intraparietal sulcus. The parieto-occipital gyrus (52) is comparable to the poorly-developed second annectant gyrus in the anterior wall of the Affenspalte of apes. In the human brain it has risen to the surface and constitutes a well-developed annex to the occipital lobe. In this connection it should be noted that excepting the perpendicular external sulcus of Bischoff, sometimes seen crossing the occipital pole, no other sulcus directly comparable to the simian Affenspalte is present in the human fetal brain at any time. Later another sulcus appears posterior to the paroccipital and parieto-occipital gyri. This is the transverse occipital sulcus (67).

The parietal lobe of anthropoid apes and man

There is little doubt about the homologies of sulci and gyri in the parietal cortex of the apes and man (figs. 35 to 42) for they present a definite anthropoid pattern which is fairly stable in the whole group. The parietal lobe is limited in front by the **central sulcus** (1), posteriorly by the anterior lip of the Affenspalte (65) in the apes and by the paroccipital and anterior occipital sulcus (51) in man. Below it is limited by the posterior limb of the **sylvian fissure** (75). It includes the cortex of three general areas, the postcentral, superior parietal, marginal and angular gyri and the associated sulci, and the precuneal gyrus on the medial surface. For convenience the paroccipital (54, first annectant) and parieto-occipital (52) gyri are here included in this connection, though they are in reality a part of the occipital lobe. In the apes they are found in the walls of the Affenspalte as the first and second annectant gyri and their homology to the gyri in the human brain is apparent. The paroccipital sulcus is situated at the bottom of the simian fossa (Affenspalte). The anterior occipital sulcus (51) is not so clear on account of the poor development of the second annectant gyrus (parieto-occipital) but coincides with the posterior border of the angular gyrus. In the human brain the Affenspalte has been unfolded by the great growth of the paroccipital and parieto-occipital (52) gyri, and the paroccipital, anterior occipital and transverse occipital sulci appear on the surface; whereas in the apes they are found in the walls and bottom of the Affenspalte.

The **postcentral gyrus** (38–40) is long and sinuous, bordered in front by the **central sulcus** (1) and behind by the **superior** (39) and **inferior postcentral sulci** (37). The three curves in the gyrus in a general way represent the upper, middle and lower parts of the gyrus. The upper part (deep sensibility for lower limb) forms the superior end. It is bounded by the posterior upturned end of the posterior cingular sulcus (27) around the end of which it joins the superior parietal gyrus. The middle part (deep sensibility for upper limb), though small and dorsally placed in the chimpanzee and gorilla, is large and occupies a middle position in the orang and man. It is usually connected with the long oblique limb of the superior parietal gyrus which is narrow and often forms a submerged convolution. The lower part (38) (deep sensibility for head and neck) is a narrow stem that widens out into a triangular, indented gyrus in the operculum which divides, to join the precentral in front and the marginal gyrus behind it. This separation is indicated by the dent in its surface and also by the **transverse postcentral sulcus** (45) in the opercular margin. In apes this pattern is stable but in man variations will be found particularly in the right hemisphere owing to the disruption of the intraparietal sulcus into several elements.

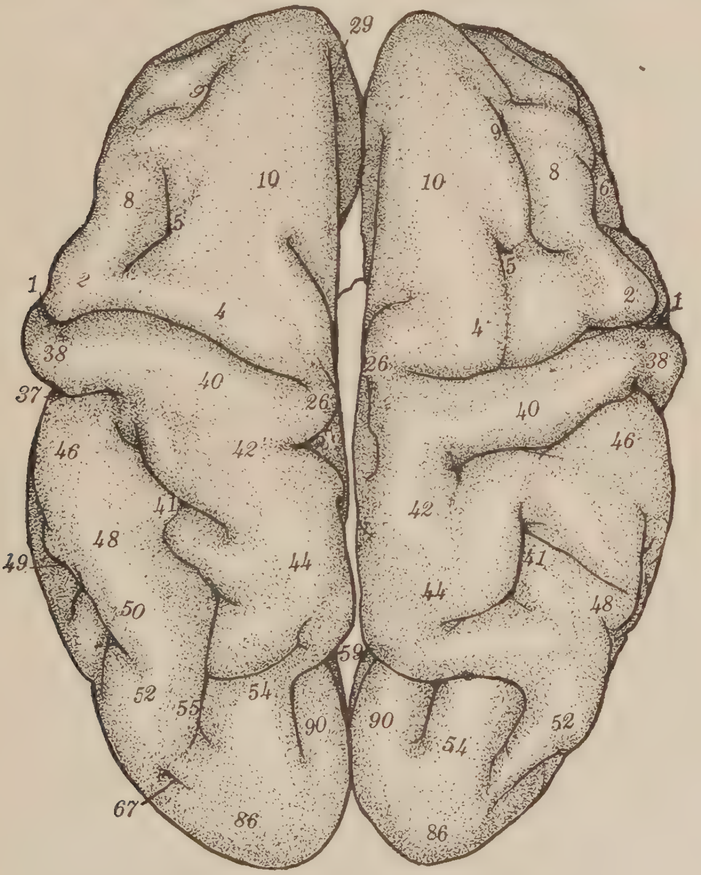

FIG. 33. Cerebrum of a seven-month human fetus, dorsal view, × 1¼.

The **superior postcentral sulcus** (39) is a short furrow that separates the upper end of the **postcentral gyrus** (40) from the **anterior superior parietal gyrus** (42). It is not found in cebus. In the baboon it is a mere depression but in the apes and man it is always present, though late in development. It is modified by variation in the superior parietal sulcus (43) and sulcus (57) in the precuneal gyrus which tends to come over the medial margin of the hemisphere.

The **superior parietal gyri** (42–44) are an irregular area of cortex bounded below by the **intraparietal sulcus** (41), in front by the superior postcentral sulcus (39), behind by the paroccipital sulcus (55) in the anterior wall of the Affenspalte of the apes. On the medial side it joins the precuneal gyrus over the medial border of the hemisphere. It is divided into a superior (42) and middle (44) gyrus by the **superior parietal sulcus** (43), which may or may not join the anterior part of the angular. Though this junction is usually submerged, in the adult brain it often forms the conspicuous **middle** (or oblique) **parietal gyrus** (44). Posteriorly this gyrus extends back to the **paroccipital sulcus** (55) in front of which, in man, it turns down to join the **parieto-occipital gyrus** (52). This gyrus is largely hidden in the Affenspalte in the chimpanzee and gorilla. In the orang and man it appears on the surface as an expansion of the superior parietal gyrus downward behind the angular gyrus from which it is separated by the anterior occipital sulcus (51). The paroccipital (55) sulcus surrounds the **paroccipital gyrus** (54) which joins the occipital cortex around the **parieto-occipital sulcus** (59). Thus the annectant gyri that form the hidden cortex of the Affenspalte in the apes are on the surface in man.

The **medial surface** of the parietal lobe is formed by the **precuneal gyri** (56–58), separated by a **precuneal sulcus** (61) which cuts it backwards. Another **parietal marginal sulcus** (57) cuts the medial margin and often extends laterally between the two **superior parietal gyri** so that they become separated into an anterior (42) and a posterior (44) part. The precuneal gyrus is bounded in front by the posterior cingular sulcus (27) and behind by the parieto-occipital sulcus (59). Below the **subparietal sulcus** (63) separates it from the **parasplenial gyrus** (62).

The **intraparietal sulcus** (41) is a deep curved cleft that separates the superior parietal gyrus (44), and also the parieto-occipital gyrus (52) in orang and man, from the marginal (46–48) and angular gyri (50). In man it is disrupted into the inferior postcentral (37), intraparietal (41), paroccipital (55) and anterior occipital (51). In simia it enters into the formation of a complete unit. Its anterior end joins the deep **inferior postcentral sulcus** (37). Its posterior end joins the **anterior occipital sulcus** (51) which extends down behind the angular gyrus or may join the paroccipital sulcus (55) in the simian sulcus (65) or Affenspalte of the lower apes. In orang and man the **transverse occipital sulcus** (67) at the bottom of the Affenspalte of the simia rises to the surface as a downward extension of the posterior end of the paroccipital sulcus and extends down behind the parieto-occipital gyrus.

The **marginal** (46–48) and **angular** (50) gyri present in apes and man a characteristic *T*-shaped convolution, the stem of which appears as an upward continuation of the **superior temporal gyrus** (68). The stem is situated between the upturned end of the sylvian fissure **marginal sulcus** (47), and the **angular sulcus** (49). With this convoluted crosspiece that leads forward it forms the **marginal gyrus** (46–48) which joins the lower end of the postcentral gyrus to form the parietal operculum. It is broad and indented in the apes. It passes back to join the **angular gyrus** (50) in the apes, and here a small connecting piece is usually seen in the human brain. The **angular gyrus** (50) lies between the angular sulcus and the **anterior occipital sulcus** (51) situated in the apes in the anterior lip of the simian sulcus or the Affenspalte (65). The lower end of the angular gyrus is narrow and joins the temporal gyri. The upper end is large, especially in the orang. In man the posterior end of the intraparietal sulcus (41) may unite with either the paroccipital sulcus (55) or the anterior occipital sulcus (51) as in apes, or by the growth of the connecting gyrus may fail to join with either. Thus the parieto-occipital gyrus (52) may appear united with either the superior parietal gyrus or the angular gyrus.

The **parietal operculum** (24–46) is formed by the union of the marginal gyrus (46) and the lower end of the postcentral (24). It is notched by the transverse postcentral sulcus (45). By apposition with the superior temporal gyrus (68) it forms the **sylvian fissure** (75). When it is raised it will be seen to be formed of a subcentral (24) and **suprasylvian gyrus** that lead medially and posteriorly and interlock with the transverse temporal gyri of the temporal operculum.

CHAPTER 6

THE TEMPORAL LOBE OF PRIMATES

IN the Carnivora we have seen that the temporal lobe was limited above by the sylvian fissure and below by the posterior rhinal fissure. An arbitrary posterior limit may be indicated by a line which joins the upper end of the posterior suprasylvian sulcus with that of the rhinal fissure. The lobe includes the cortex of the posterior sylvian, ectosylvian and the lower part of the posterior suprasylvian gyri as well as the polar gyrus that borders the posterior rhinal fissure.

In the Primates the temporal lobe is bounded above by the sylvian fissure (75), over the temporal pole by the posterior rhinal fissure (93), on the medial side by the collateral sulcus (83). The anterior occipital sulcus (in the lower end of the Affenspalte), joined by an arbitrary line with the collateral fissure, may be taken as the posterior limit. Along this line a deep, though irregular, folding occurs in the human brain. In the Primate brain three parallel temporal gyri are recognized, a superior, middle and inferior gyri, separated by superior and inferior temporal sulci but joined at the pole. In man there is much crowding and irregularity of gyri and sulci and the middle temporal region is greatly enlarged.

The origin of the sylvian fissure in Primates is indicated in the brain of the lemur (fig. 24). Compare this with the conditions in the bear (fig. 22). In the lemur the anterior suprasylvian gyrus (38) has been pushed back so as to cover the suppressed (muzzle) area called the anterior ectosylvian (38b) in the bear. Thus the anterior part of the suprasylvian sulcus of Carnivora has been transformed into the sylvian fissure of the Primates (75) while the posterior part of the suprasylvian sulcus (69) is preserved as the superior temporal sulcus of Primates. For explanation of numbers see page 27.

The temporal lobe of Cebidae, figures 25 to 28

The **superior temporal gyrus** (68) is long and distinct, situated between the **superior temporal** (69) and **sylvian** (75) **sulci.** Its lower end joins the polar gyrus (74). Its upper end narrows to a point and sinks into the posterior end of the sylvian sulcus to join the marginal (46). In lagothrix this union is on the surface due to the development of the anterior part of the marginal gyrus (46). When the lips of the sylvian sulcus are separated a **transverse temporal gyrus** (78) is seen on the upper or opercular surface of the superior temporal gyrus (68). This is the auditory area.

The **superior temporal sulcus** (69) is a long cleft that runs through the length of the lobe and is continuous with the **angular sulcus** (49) which separates the **angular** (50) from the **marginal gyrus** (48). In cebus due to the lack of a well-developed anterior marginal gyrus (46) the angular sulcus (49) appears to join the sylvian fissure (75) as well as the superior temporal sulcus (69). A temporal **polar gyrus** (74) is formed along the rhinal fissure by a union of the anterior ends of the three temporal convolutions.

The **middle temporal gyrus** (70) is a large smooth convolution. Near the temporal pole a shallow **middle temporal sulcus** (71) separates it from the inferior temporal gyrus (72). Back of this sulcus the two gyri form a common convolution over the border of the hemisphere. The posterior end joins a large triangular occipito-temporal gyrus (76) that unites above with the angular gyrus (50) and behind with the lower end of the occipital operculum over the **inferior occipital sulcus** (77). On the medial or tentorial surface the **inferior temporal sulcus** (73) separates the inferior temporal gyrus from the combined anterior fusiform and lingual gyrus (80). A broad continuity (82) between the fusiform and the hippocampal gyri exists behind the rhinal fissure resembling the conditions found in the Carnivora and rodents. Behind this continuity the fusiform gyrus (80) is separated by the **collateral sulcus** (83) from the **lingual gyrus** (84). In the Cebidae the collateral sulcus is incomplete and its anterior end tends to join the inferior temporal sulcus by passing diagonally across the fusiform gyrus.

The temporal lobe of the baboon, figures 29 and 30

The temporal lobe has a well-defined primate pattern. Its resemblance to the brain of Cebidae on the one hand and the apes and man on the other is readily seen.

The **superior temporal gyrus** (68) is a long straight one that forms the inferior boundary of the **sylvian sulcus** (75). It is large in its anterior extent and narrow posteriorly where it joins the marginal gyrus (48). This junction, hidden in the cebus, is on the surface in the lagothrix, macacus and baboon. When the gyrus is raised from the parietal operculum a **transverse temporal gyrus** (78) is seen on its upper concealed surface. This gyrus constitutes the auditory area.

The **superior temporal sulcus** (69) is a deep cleft that separates the superior (68) from the middle temporal (70) gyri. Posteriorly it is continued into the **angular sulcus** (49) which separates the angular (50) from the marginal (48) gyrus. This union is a simian characteristic, but in the higher apes it becomes evident that these are separate furrows. In man this continuity is often disrupted so that the independence of the two sulci is clearly demonstrated. They may be regarded as limiting sulci for the auditory (68) and marginal (48) area in front and for the angular (50) and temporal (70) area behind.

The **middle temporal gyrus** (70) is a narrower convolution imperfectly separated from the **inferior temporal gyrus** (72) by two shallow furrows, the **middle temporal sulci** (71). Its convoluted posterior end joins the **occipito-temporal gyrus** (76) around the temporal end of the **inferior occipital sulcus** (77). An **inferior temporal sulcus** (73) on the tentorial surface separates the inferior temporal gyrus (72) from the **fusiform gyrus** (80). Both gyri run back towards the occipital pole. The fusiform gyrus (80) is separated from the **lingual gyrus** (84) by the **collateral sulcus** (83). The lower end of the fusiform gyrus has a broad connection (82) with the hippocampal gyrus comparable to that seen in cebus and Carnivora. Around the temporal pole the temporal gyri unite to form the **temporal polar gyrus** (74).

In the macacus and baboon the **inferior occipital sulcus** (77) is a composite furrow that separates the convoluted **occipito-temporal gyrus** (76) and the **inferior occipital gyrus** (88) from the long posterior end of the inferior temporal gyrus (72) as it reaches backwards to the occipital pole. In the higher apes the occipito-temporal sulcus is united either with the middle or inferior temporal sulci. Such a union is anticipated in the macacus and baboon by shallow connecting depressions.

The temporal lobe of a seven-month fetus, figures 31 to 34

In the human fetus the growing cortex repeats the primitive Primate pattern. The **sylvian sulcus** (75) is well formed. Its posterior upturned end, the marginal sulcus (47), cuts into the marginal gyrus (48). The **superior temporal gyrus** (68) as in apes forms the lower border of the sylvian sulcus (75) and its posterior upturned end is continued into the marginal gyrus (48). Its anterior end joins the cortex of the **temporal polar gyrus** (74) which is yet broad and smooth and unites the temporal gyri lateral to the **posterior rhinal fissure** (93). On its upper concealed surface are found the anterior and posterior **transverse temporal gyri** (78).

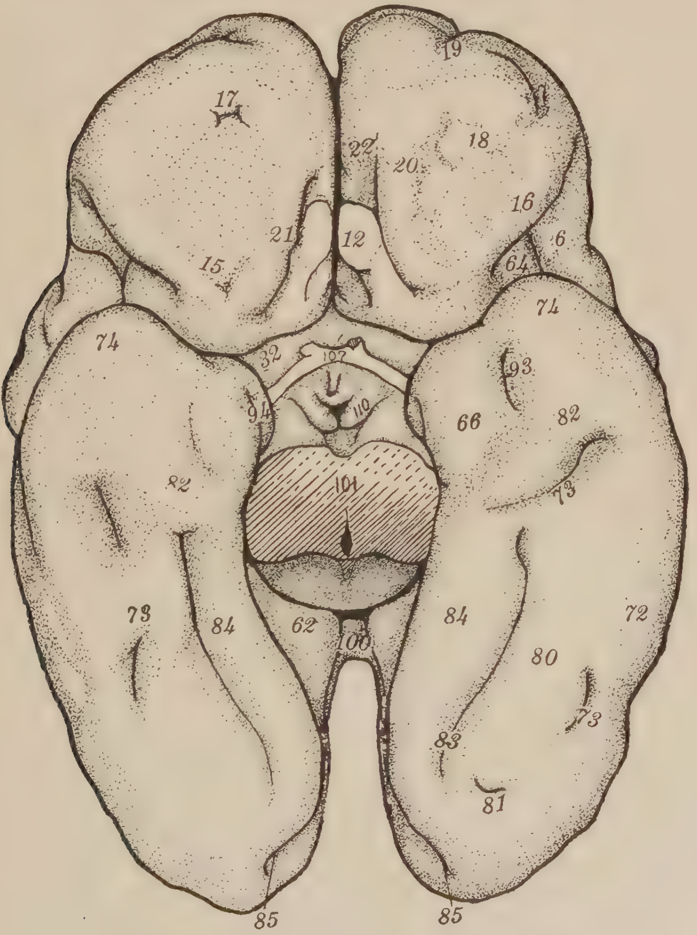

FIG. 34. Cerebrum of a seven-month human fetus, ventral view, × 1½.

The **superior temporal sulcus** (69) is a deep cleft that separates the superior from the **middle temporal gyrus** (70). Posteriorly as in apes it joins the **angular sulcus** (49) which separates the posterior limb of the **marginal gyrus** from the **angular gyrus** (50). In some fetuses the angular and superior temporal sulci are separated at the lower end of the angular gyrus. In this fetus the angular gyrus is well developed on the right side but less so on the left. Behind it, another vertical cleft, the **anterior occipital sulcus** (51) separates the angular (50) from the parieto-occipital gyrus (52). It will be noticed that in its formation this sulcus is confluent with the angular sulcus (49), over the depressed lower end of the angular gyrus (50). By this sulcal formation the enlarged posterior end of the middle temporal gyrus (70) is circumscribed. It has been shown that the **parieto-occipital gyrus** (52), so distinctive of the human cortex, is hidden in the anterior wall of the Affenspalte (65) in the simia and comes partly to the surface only in the higher apes.

The **middle** (70) and **inferior** (72) **temporal gyri** form together a large expanse of cortex indented at this stage of development by two shallow **middle temporal sulci** (71). Posterior and in series with these is a small furrow (87) which may be the **lateral occipital** or the **occipito-temporal sulcus** (77) of the adult brain (fig. 43).

On the tentorial surface the **posterior rhinal fissure** (93) is seen separating the **temporal polar gyrus** (74) from the **pyriform area** (66). The deep **collateral sulcus** (83) separates the fusiform gyrus (80) from the **lingual gyrus** (84). More laterally two short inferior temporal sulci (73) separate the **inferior temporal gyrus** (72) from the **fusiform gyrus** (80). The fusiform (80) and inferior temporal (72) gyri extend back to the occipital pole as in the simia and here on the right side an **inferior occipital sulcus** (77) is appearing.

The temporal lobe of apes and man, figures 35 to 44

The **sylvian sulcus** (75) in the anthropoid apes and man ends in an upturned extremity, the marginal sulcus (47). Its lower boundary is formed by the **superior temporal gyrus** (68) which is a long well-developed convolution. When drawn down, there are seen on its upper surface an **anterior** and a **posterior transverse temporal gyrus.** The anterior joins the front half of the superior temporal gyrus (68) and the posterior joins the posterior half. A deep incision, often seen on the surface in orang and man, indicates the outer end of the sulcus that separates the two. It will be seen that in man this is much farther forward than in the apes which is explained by the greater development of the posterior half of the superior temporal gyrus and of the posterior transverse temporal gyrus. This gyrus is continued into the posterior part of the marginal gyrus (48) back of the marginal sulcus (47). The **superior temporal sulcus** (69) separates the anterior part of the gyrus from the **middle temporal gyrus** (70) and may consist of two parts in the human brain. The **angular sulcus** (49) separates the angular (50) and marginal (48) gyri, and running down separates the posterior part of the superior temporal (68) from the posterior part of the middle temporal gyrus (70). In apes the angular sulcus (49) is confluent with the superior temporal sulcus (69) although the deep annectant gyri indicate a connection between the posterior ends of the two temporal gyri. So great is the growth in this region in man that the annectant gyri often come to the surface and the continuity of the superior temporal and angular sulci is broken. This is a human feature. In the anthropoid apes the lower end of the angular sulcus extends down behind the posterior end of the middle temporal gyrus (70).

The **middle temporal gyrus** (70) is partly separated from the **inferior temporal gyrus** (72) by two shallow, oblique **middle temporal sulci** (71) which may remain separate as is usual in man or may coalesce as in the orang. On account of the crowding of gyri in this region an irregular pattern is produced in the human brain and the sulci have an oblique position often cutting the middle temporal gyrus into several segments. In the chimpanzee (fig. 39) and gorilla the middle temporal sulcus (71) joins the **inferior occipital sulcus** (77). In the other apes the latter most often joins the **inferior temporal sulcus** (73) although submerged gyri bridge this union. The **inferior temporal sulcus** (73) is situated near the border of the hemisphere on the tentorial surface and most often joins the **inferior occipital sulcus** (77). It is a short but well-defined furrow that separates the **inferior temporal gyrus** (72) from the narrow **fusiform gyrus** (80) on the medial surface. The **temporal polar gyrus** (74) unites the temporal gyri and the fusiform along the tip of the temporal pole. In some cases it is limited by one or two **temporal polar sulci.** In the apes these are usually confluent with the superior temporal sulcus. Back of the pyriform lobe (66) the fusiform gyrus (80) is united with the **hippocampal gyrus** (104) at 82 (fig. 40). Behind this union the **collateral sulcus** (83) separates the fusiform (80) from the **lingual gyrus** (84). In the human brain the annectant gyri that unite the fusiform and the posterior end of the middle temporal and the occipito-temporal gyri are greatly developed so that the continuity of the inferior and middle temporal and the inferior occipital sulci so common in the apes is broken.

The **inferior occipital sulcus** (77) is well-defined in the apes (fig. 39), and unites over the annectant gyri with the inferior temporal sulcus or with the middle temporal sulcus. The angular sulcus extends down and unites above this sulcus with the **occipito-temporal gyrus** (76). The inverted *L*-shaped convolution thus formed is characteristic of apes. In the human brain it (76) undergoes considerable growth and crowding but is included between the **anterior occipital** (51), **lateral occipital** (87) and **inferior occipital** (77) sulci, and its continuity with the middle temporal (70) in front and the inferior lateral occipital (88) gyrus is usually kept. The inferior occipital (77) and the inferior temporal sulci are separated by the great growth of annectant gyri that join the posterior part of the inferior temporal gyrus (76) with the fusiform (80) over a deep fold in the inferior border of the brain.

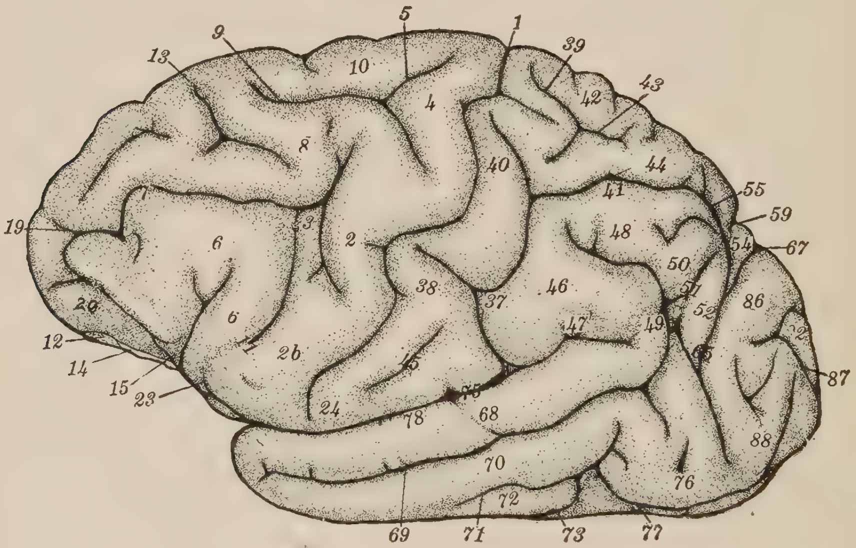

FIG. 35. Cerebrum of a gorilla, lateral view, × 1.

The insular area

The **insular area** or island of Reil is a triangular area of cortex covered over by the sylvian gyri in the Carnivora and by the marginal and superior temporal gyri in the simia and man. In front it is covered by the lower ends of the post- and precentral, the inferior frontal and the orbital gyri. The sylvian fissure (75) in Primates is therefore an opening to a deep fossa, the bottom of which is formed by the insular area. This area is bordered below by the rhinal fissure, and by an extensive circular sulcus under the opercula. The insular cortex covers the outer surface of the corpus striatum. This is a solid structure in the basal wall of the hemisphere. The remainder of the hemisphere is vesicular and in its expansion grows over the insular cortex in the form of the opercula. In the Carnivora the insula is a triangular piece of cortex at the bottom of the sylvian sulcus. It is overlapped by the sylvian gyri and upper end of the temporal polar gyrus. The lower border is formed by the rhinal fissure. A deep circular sulcus forms its posterior and anterior borders deep under the covering gyri. The insular cortex joins the pyriform across the bottom of the rhinal fissure. It has a long insular gyrus posteriorly and one or two short insular gyri anteriorly.

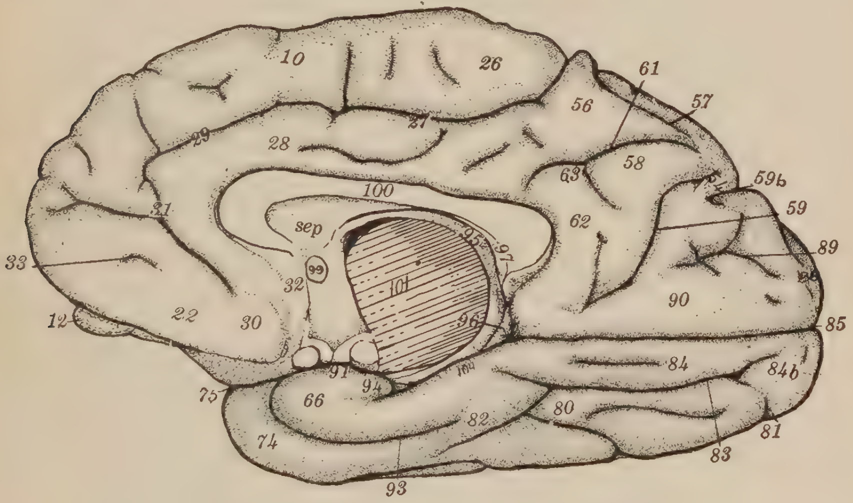

FIG. 36. Cerebrum of a gorilla, medial view of right half, × 1.

In cebus, macacus and baboon the insula is covered by the frontal parietal opercula and the superior temporal gyrus. It is a smooth, somewhat elongated area of cortex surrounded by the circular sulcus. Anteriorly there is a feebly developed fronto-orbital operculum.

In apes and man the insular area progressively enlarges so that during development it is at first only partially covered by three opercula. Its rhinal border becomes short and curved and the rhinal fissure is lost in man. When the gyri which form the lips of the sylvian sulcus or opercula of the insula are separated there are seen on the upper surface of the superior temporal lobe the anterior and posterior transverse temporal gyri separated by a corresponding sulcus. This is the auditory area of the brain and it overlies the long insular gyrus. On the underside of the marginal gyri will be seen the suprasylvian gyrus. The subcentral and inferior frontal gyri complete the superior operculum. In front is the orbital operculum. Thus the island is a triangular area surrounded by the circular sulcus which consists of the temporal, superior and orbital portions.

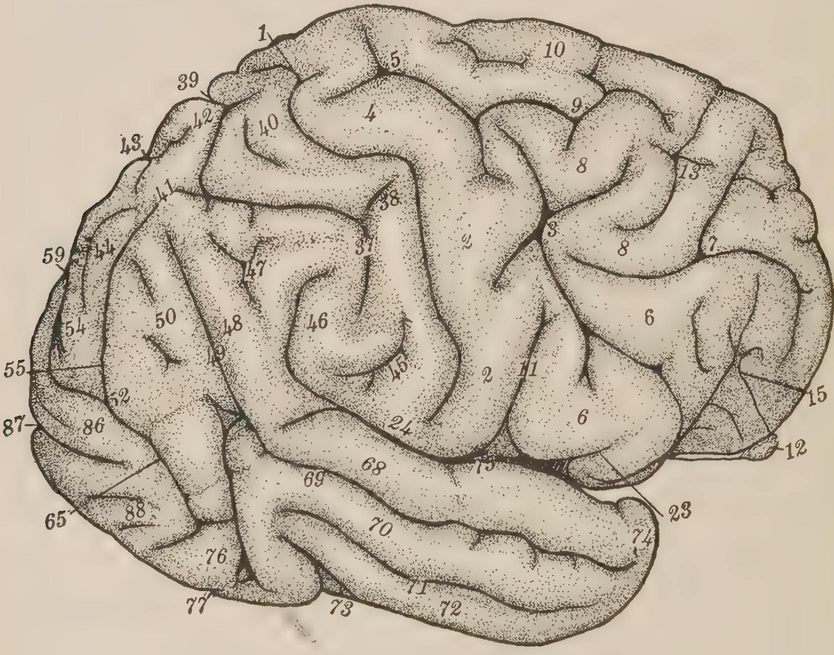

FIG. 37. Cerebrum of an orang, lateral view, × 1.

In apes the fronto-orbital operculum is poorly developed, but a cleft, the **ascending limb** (23) of the sylvian sulcus has already appeared and a distinct diagonal sulcus (11) is always seen. In apes the posterior part of the inferior frontal gyrus is prominent. In man (figs. 31, 43) it is usually a narrow upcurved loop covered by the greatly developed anterior triangular part which is separated from the orbital operculum by the **horizontal limb** (25) of the sylvian sulcus. In the apes this separation does not exist. In front of the orbital operculum is the **fronto-orbital sulcus** (15) reduced and often disrupted in man by the growth of the triangular part of the operculum.

The insular cortex in man is divided by a **central insular sulcus** into a long posterior gyrus and several short anterior insular gyri. The rhinal border is greatly shortened and curved.

The early **formation of the sylvian fossa** is best shown in the Lemurs (fig. 24). It is seen that the superior temporal gyrus (68) is enlarged and some of its cortex has been turned in and disappears from the surface. In the higher Primates this forms the transverse temporal gyrus (78). In the same way the inferior postcentral gyrus (38) has overgrown this region from above and the cortex (38b) is submerged. A similar infolding is seen in some Carnivora (fig. 22) where the anterior ectosylvian gyrus (38b) is submerged. In some Ungulata (fig. 18) the sylvian gyri (78 and 78b) are also submerged. The posterior part of the insular cortex of Primates is thought to be most nearly comparable to the anterior sylvian gyrus (78b) of the lower orders of Mammals (see pages 24 and 43).

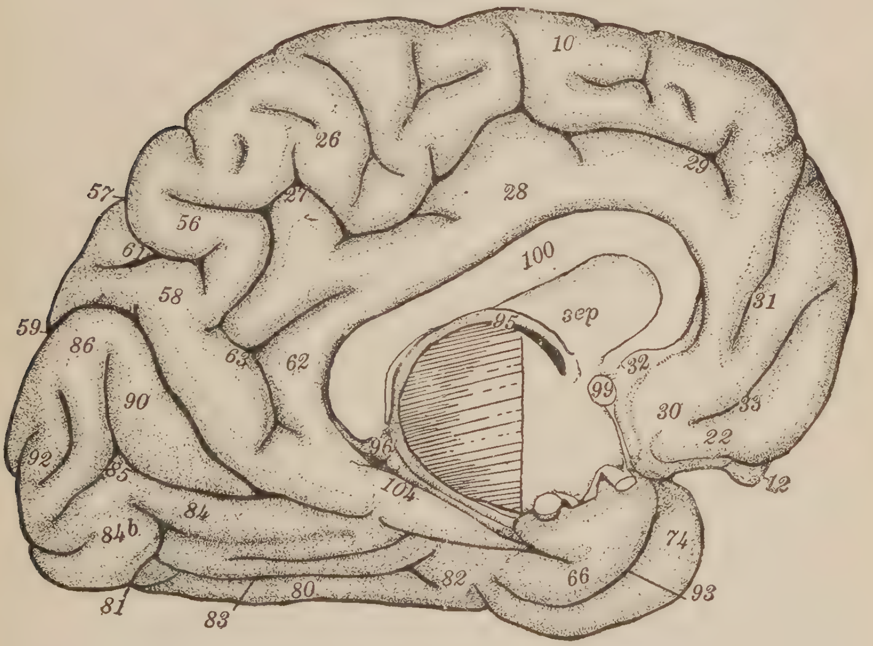

Fig. 38. Cerebrum of an orang, medial view of right half, × 1⅛.

CHAPTER 7

THE OCCIPITAL LOBE OF PRIMATES

A DISTINCTIVE feature of the Primate brain is the great development of the occipital lobe. This region of the brain is dominated by the **visual area** which is formed by the cortex of the calcarine fissure (85) and the gyri which surround it. In the apes it is the expansion of this visual area and its surrounding gyri which causes the formation of the occipital operculum (86–88) and the simian sulcus (65) or Affenspalte. In man the growth of the visual cortex is pushed still further and in addition great connecting gyri, the parieto-occipital (52) and the occipito-temporal (76), are developed in the region of the simian sulcus (65), so that the latter never actually appears in the human brain, if we except the rare occurrence in the fetus of its probable homologue, the perpendicular external sulcus of Bischoff. For explanation of numbers see page 27.

The occipital lobe of Primates is bounded on the medial surface by the parieto-occipital sulcus (59), on the lateral surface by the simian sulcus (65) or Affenspalte, in the human brain by the anterior occipital sulcus (51), and on the ventral or tentorial side by the inferior occipital (77), the transverse collateral (81) and the collateral sulcus (83). Thus the lobe includes the cortex of the calcarine sulcus, the lingual, cuneal, lateral, occipital, occipito-temporal, paroccipital and parieto-occipital gyri and the bordering sulci.

A possible interrelation between the expansion of the occipital lobe and the frontal lobe in Primates is to be kept in mind (p. 37).

The occipital lobe of Cebidae, figures 25 to 28

The occipital lobe of Cebidae presents the simian pattern of this region in a simple form. On the lateral surface it is limited by the parieto-occipital (59), the posterior limb of the intraparietal (41) and the transverse occipital sulcus (65) or Affenspalte.

The lateral occipital surface is formed by a smooth cap of cortex, the lateral occipital gyri (86–88). The anterior margin of this area is bordered by the **transverse occipital sulcus** (67) and corresponds to the posterior lip of the Affenspalte (65) of the higher apes. It may appear in two parts (67 and 65), a condition comparable to that usually seen in the human brain. Behind the ends of this sulcus occur small limiting sulci. In lagothrix the forked lateral occipital sulcus (87) separates the two lateral occipital gyri as in the apes. In Cebidae the true Affenspalte (65) is in the process of formation and the **paroccipital gyrus** (54) is seen on the surface bordering the parieto-occipital sulcus (59). It unites around the posterior extremity of the intraparietal sulcus (41) with angular gyrus (50) in cebus, but with the superior parietal gyrus (44) in lagothrix. Below this is the very small parieto-occipital gyrus (52) partly hidden in the anterior wall of the transverse occipital sulcus (65) or Affenspalte. Below this gyrus is the **occipito-temporal gyrus** (76) united posteriorly with the lower end of the lateral occipital gyrus (88) below the Affenspalte. Thus the Affenspalte of Cebidae presents an early stage in the evolution of the opercular form of the Affenspalte of higher apes.

The **inferior occipital sulcus** (77) separates the lateral occipital (88) from the occipito-temporal (76) gyrus.

The **calcarine fissure** (85) appears as a deep furrow on the medial surface. Its anterior end separates the upper end of the hippocampal gyrus (104) from the parasplenial gyrus (62). Its posterior end forms a *T*-shaped terminus near the medial margin of the hemisphere. The fissure is bordered below by the **lingual gyrus** (84), above by the **cuneal gyrus** (90) and its cross piece is bordered behind by the medial margin of the **lateral occipital gyri** or occipital polar-gyrus (92).

The cortex of the walls of the calcarine fissure constitutes the **visual area** (striate area) and the surrounding gyri constitute a fringe of cortex, the peristriate area. Around this, limiting sulci occur. Below the anterior part of the lingual gyrus (84) is the collateral sulcus (83), and below the tip of the occipital pole there is the **inferior occipital sulcus** (77). In the cuneal gyrus (84) there is a limiting cuneal sulcus (89) which separates the gyrus into two parallel parts that border the parieto-occipital sulcus (59). The anterior end of the cuneal gyrus (90) unites with the parasplenial (62) and its upper part with the precuneal gyrus (58), as may be seen in cebus.

The occipital lobe of the baboon, figures 29 to 30

The parietal lobe of the baboon (the brain of macacus rhesus may be used instead) presents three surfaces, a lateral, a medial and an inferior. It is limited on the lateral side by the simian sulcus (65) or Affenspalte and on the medial side by the parieto-occipital sulcus (59). On the inferior surface it is limited by the hippocampal gyrus (104). The fusiform (80) and inferior temporal (72) gyri extend into both temporal and occipital regions. Across these passes the transverse collateral sulcus (81).

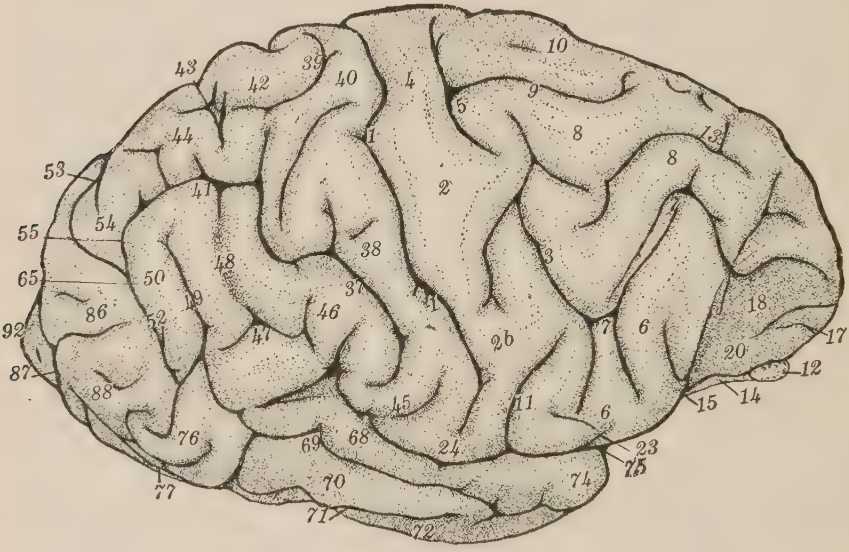

FIG. 39. Cerebrum of a chimpanzee, lateral view, ×1⅛.

The calcarine fissure (85) on the medial surface extends from the hippocampal gyrus (104) to the tip of the occipital lobe where it ends in a *T*-shaped manner. The anterior part of the sulcus is deep but its shallow end cuts across the upper end of the **hippocampal gyrus** (104) and separates it from the **parasplenial gyrus** (62).

The **lingual gyrus** (84) forms the lower boundary of the calcarine fissure. It consists of an anterior and a posterior part. The broad anterior part joins the hippocampal gyrus (104). Its narrow posterior end becomes hidden in the calcarine fissure, but soon emerges to join the posterior part (84b) which forms the tip of the occipital pole. The anterior part of the lingual gyrus is limited below by the **collateral sulcus** (83) which separates it from the **fusiform gyrus** (80).

The cortex of the lingual and cuneal gyri and the walls of the calcarine fissure form the **visual area** for which the collateral (83), transverse collateral (81) and parieto-occipital (59) are limiting sulci.

The cuneal gyrus (90) forms the upper boundary of the calcarine fissure, around the polar end of which it bends to become continuous with the lingual gyrus (92). It represents the upper wall of the visual area. The **parieto-occipital sulcus** (59) is a deep cleft that separates the cuneal gyrus (90) from the precuneal (58). The lower end of the sulcus (59) does not join the calcarine so that the cuneal gyrus (90) is continued directly into the parasplenial (62) and precuneal (58) gyri. The dorsal end of the parieto-occipital sulcus (59) is surrounded by the paroccipital gyrus (54) in the upper part of the Affenspalte (65).

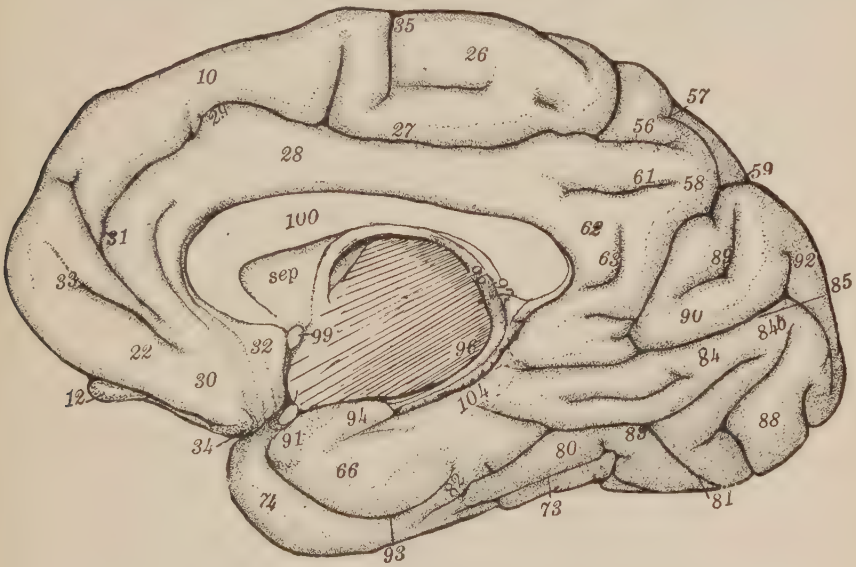

FIG. 40. Cerebrum of a chimpanzee, medial view of right half, × $1\frac{1}{8}$.

Along the lateral border of the occipital lobe is seen the deep **inferior occipital sulcus** (77) which separates the long occipital end of the **inferior temporal gyrus** (72) from the inferior lateral occipital gyrus (88) and in front from the **occipito-temporal gyrus** (76). The latter is seen as a prominent *Y*-shaped convolution which unites the lateral occipital (88) with the middle temporal (70) and is joined from above by the angular gyrus (50).

The lateral occipital surface is formed by an expanse of smooth cortex separated by the **lateral occipital sulcus** (87) into a **superior** (86) and an **inferior lateral occipital gyrus** (88). This sulcus (87) ends at the occipital pole below the *T*-shaped end of the calcarine fissure. Above it, is usually seen another shallow furrow which is the forerunner of the upper branch of the lateral occipital sulcus. The inferior lateral occipital gyrus (88) at its anterior end joins the occipito-temporal gyrus (76) around the lower end of the Affenspalte (65).

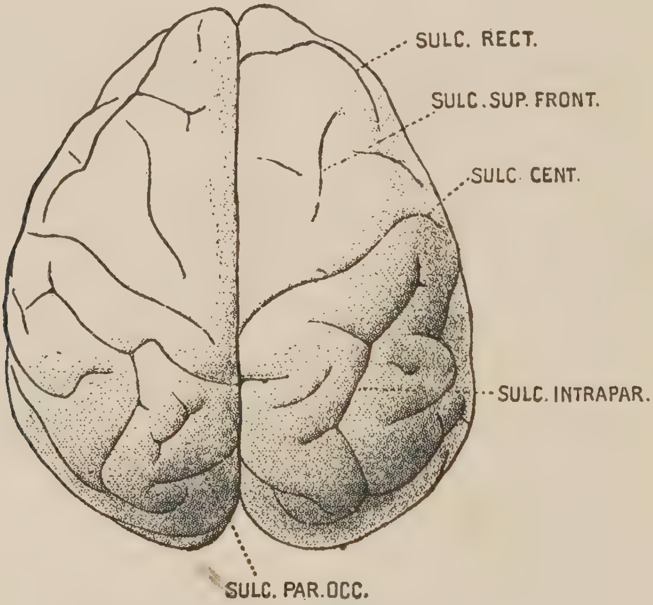

FIG. 41. Cerebrum of a gibbon, dorsal view, × 1.
From G. E. Smith.

The simian sulcus (65) or Affenspalte is a deep cleft formed between the angular gyrus in front, and the lateral occipital gyri behind. The cleft is produced by an overgrowth of the lateral occipital gyri which forms the posterior part of a rapidly expanding (peristriate) area around the visual area. When the cleft is opened the **transverse occipital sulcus** (67) will be seen under the margin of the lower lip. In the anterior wall of the cleft connected with the lower part of the angular gyrus (50) will be seen the second annectant or **parieto-occipital gyrus** (52). Above this will be seen the first annectant or **paroccipital gyrus** (54) looping sharply around the dorsal end of the parieto-occipital sulcus (59). The gyrus is circumscribed by a shallow **paroccipital sulcus** (55). How this sulcus may join the intraparietal, the transverse occipital or the anterior occipital can readily be seen.

The occipital lobe of a seven-month human fetus, figures 31 to 34

The medial occipital cortex is folded over a deep horizontal cleft, the **calcarine fissure** (85). Its lower wall is the **lingual gyrus** (84). Ventral to this is seen the deep **collateral sulcus** (83). The upper wall of the calcarine sulcus is formed by the **cuneal gyrus** (90). The posterior end of the calcarine fissure cuts the occipital pole and is still straight. A smooth **lateral occipital area** (86–88) forms a cap-like tip of the occipital pole.

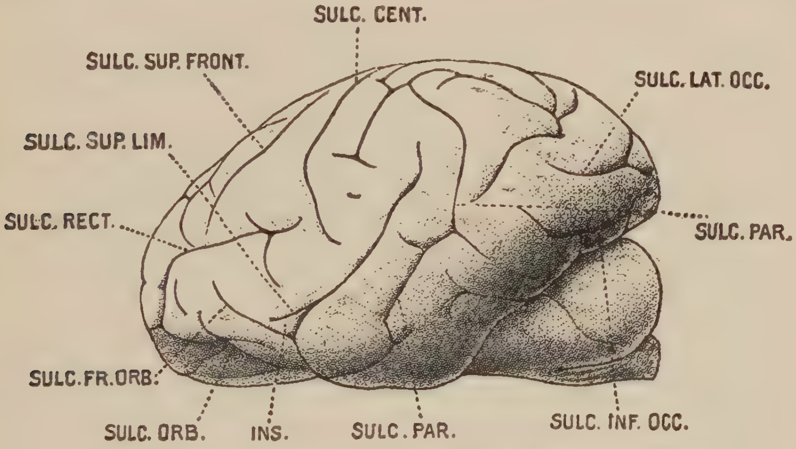

FIG. 42. Cerebrum of a gibbon, lateral view, × 1.
From G. E. Smith.

The **parieto-occipital sulcus** (fig. 33, 59) is a well-defined cleft in front of the cuneus that joins the calcarine fissure (85). Dorsally it cuts the border of the lobe and is surrounded by the **paroccipital gyrus** (54). This gyrus is bounded laterally by the **paroccipital sulcus** (55) which is seen to join the parieto-occipital sulcus on the right side, but on the left side its complete independence is evident. This sulcus (55) effects a separation between the paroccipital gyrus (54) and the parietal gyrus (44) and parieto-occipital gyrus (52).

The great development of the **parieto-occipital gyrus** (52) on the lateral surface is a striking feature. Its upper end joins either the angular as on the left side or both angular and parietal gyri as on the right side. A small sulcus at its lower end is probably the anterior end of the **lateral occipital sulcus** (87). The great size of the parieto-occipital gyrus (52) and absence of a simian sulcus (65) or Affenspalte are to be noted as special human features.

The occipital lobe of apes and man, figures 37 to 44

The occipital lobe in apes is bounded on the lateral surface by the ape cleft, simian sulcus or Affenspalte (65). This is formed by an overgrowth of the lateral occipital gyri (86–88) in the form of an operculum which partially conceals the paroccipital (54) and parieto-occipital gyri (52) in front of it. In this respect the human brain assumes a pattern more like that of cebus, for the Affenspalte is never formed (not even in the fetus) and in its stead appears the transverse occipital sulcus (67) which is comparable to the furrow seen under the posterior lip of the Affenspalte in the brain of apes. Hence in the human brain the paroccipital (54) and the parieto-occipital (52) gyri appear on the surface as do their rudiments in cebus.

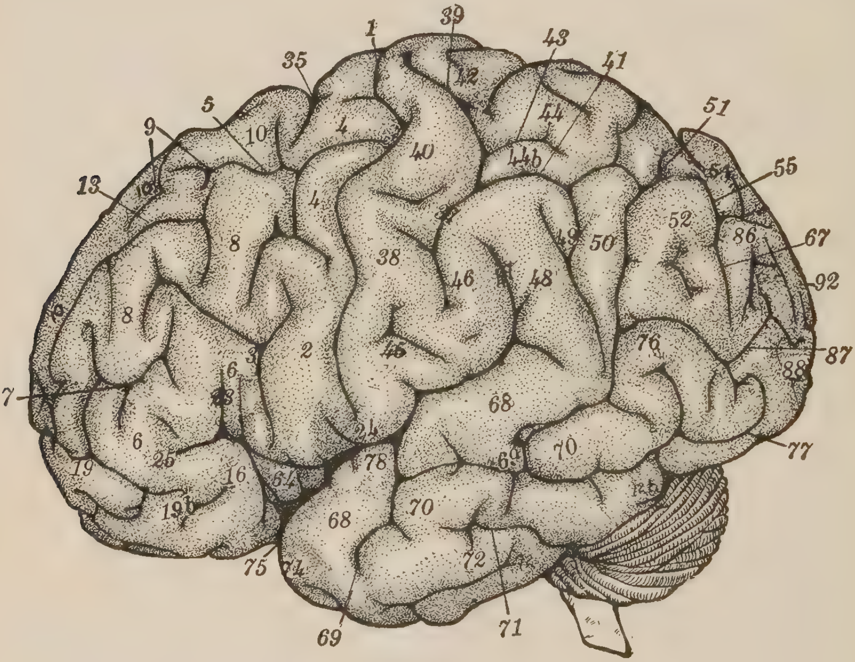

Fig. 43. Cerebrum of a newborn babe, lateral view, × 1.
For explanation of numbers see page 27.

The **calcarine fissure** (85) is a deep cleft on the medial surface of the occipital lobe. Its anterior end separates the hippocampal (104) from the parasplenial gyrus (62). Its posterior end (excepting the gorilla, in which it is straight) ends in a *T*-shaped manner above the occipital pole. It is convenient to divide it into an anterior and a posterior part. In the gorilla and orang its stem is straight but in the chimpanzee and in the human brain it is flexed sinuously due to the greater growth of its posterior part. The cortex that forms the walls of the sulcus constitutes the **visual area.**

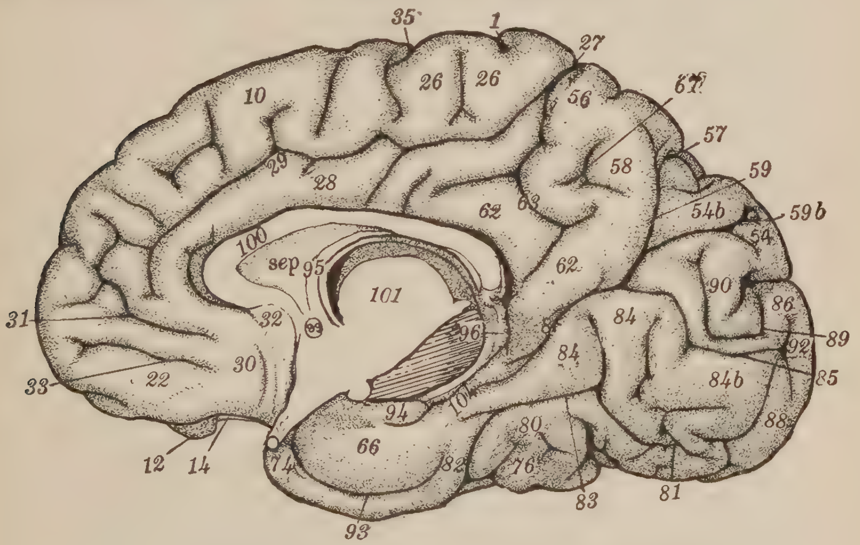

FIG. 44. Cerebrum of a newborn babe, medial view of right half, × 1.

The **lingual gyrus** (84) forms the ventral border of the calcarine fissure. An anterior and a posterior part are recognized. The anterior part is separated from the fusiform gyrus (80) by the **collateral sulcus** (83). Behind the end of this sulcus the lingual (84) gyrus forms a *T*-shaped lobule of cortex (84b) small in the apes but large and prominent in the human brain. The occipital end of the lingual gyrus (84b) forms the tip of the occipital lobe. It is here continuous with the posterior end of the **inferior lateral occipital gyrus** (88). The latter gyrus is separated from the inferior temporal gyrus (72) by the inferior occipital sulcus (77). The transverse collateral sulcus (81) in the lower apes is confluent with the inferior occipital sulcus (77) while in the gorilla, orang and man, as the polar area expands, it (81) becomes an independent furrow.

The cuneal gyrus (90) forms the upper border of the calcarine fissure. It is a wedgelike gyrus. Its posterior end joins the **superior lateral occipital gyrus** (86) at the pole, and its anterior end joins the parasplenial (62) and paroccipital (54) gyrus. In the chimpanzee, gorilla and man the gyrus is doubled by the **cuneal sulcus** (89) and the union with the parasplenial (62) and the paroccipital (54) gyri is usual on the medial surface so that there is no deep connection between the medial parieto-occipital (59) and calcarine (85) fissures, but in the orang and man and sometimes in the chimpanzee, such a connection exists. In the human brain the cuneal gyrus (90) is divided as in the chimpanzee and gorilla by a **cuneal sulcus** (89). The connection of the gyrus with the parasplenial (62) is usually indicated by a deep connecting gyrus above the junction of the calcarine (85) with the medial parieto-occipital sulcus (59). It sometimes happens that the anterior part of the paroccipital sulcus in man appears as a deep cleft on the medial surface so as to resemble the double parieto-occipital sulcus of simia. In such cases a large **paroccipital gyrus** (54) appears in front of the dorsal parieto-occipital sulcus (59b) as is usual in the chimpanzee. In such cases there is a misleading resemblance of the human dorsal parieto-occipital sulcus (59b) to the simian calcarine fissure as in figure 44.

The **parieto-occipital sulcus** (59) is a deep cleft that appears in the medial margin of the hemisphere between the cuneal (90) and precuneal (58) gyri. It is a deep limiting cleft between the occipital (visual) and parietal (general sensory) cortex produced by the growth tension of the posterior (occipital) division of the fibers of the corpus callosum. The **paroccipital gyrus** (54) forms its border on the lateral side. In apes the cuneal gyrus (90) borders it on the medial side uniting the cuneal with the parasplenial and paroccipital. In the chimpanzee this union is sometimes depressed. In the orang this is the usual condition. In the human brain this union becomes a deep annectant gyrus seldom seen on the medial surface and hence the parieto-occipital sulcus (59) joins freely with the calcarine (85).

In the lateral surface the large lateral occipital area is cleft by a *Y*-shaped furrow, the **lateral occipital sulcus** (87) which separates it into three gyri — the **superior lateral occipital gyrus** (86) above, the **inferior lateral occipital gyrus** (88) below, and the **occipital polar gyrus** (92) between the limbs of the fork of the sulcus. This polar gyrus (92) forms the crescent-like posterior boundary of the terminal crosspiece of the calcarine fissure. In the gorilla and orang secondary sulci appear around the polar gyrus (92) and join the lateral (87). In the human brain the parts of the **lateral occipital sulcus** (87) are often disrupted, but in many cases the simian pattern is reproduced so that the two parts of the simian Affenspalte can be recognized in front of the lateral occipital gyri.

The **simian sulcus** or Affenspalte (65) is formed at the anterior margin of the lateral occipital gyri (86–88) by their overgrowth over the paroccipital (54) and parieto-occipital gyri (52). These gyri are in the anterior part of the cleft wholly or partially hidden in the typical simian brain. In higher apes they rise to the surface. It is a characteristic of the human brain that the parieto-occipital gyrus (52), so rudimentary in the simia, is so greatly developed that a true simian Affenspalte is never formed across this barrier. In man it is replaced by two sulci, an upper **transverse occipital sulcus** (67) and **lateral occipital sulcus** (87) which in man extends further forward so that its front end separates the **parieto-occipital** (52) from the occipito-temporal gyrus (76).

Theory of formation of cerebral patterns

There is evidence that the cerebral cortex of the lowest smooth brained Mammals has acquired definite afferent connections from the region of the face and from such sense organs as the eyes, ears, skin and muscles. Soon these streams of afferent sensibilities come to dominate separate regions of the cortex which thus become the functional areas. The location of these areas in a primitive Mammal is shown in figure 313 from G. E. Smith (The Lancet, 1910). The expansion of the cortex in higher Mammals proceeds far beyond this stage with the formation of numerous sulci and gyri.

In the course of its growth the cortex does not increase in thickness beyond a certain point, but its expansion is attained largely by an increase in its superficial extent and by folding. The manner of folding is not haphazard, but is a result of the growth and expansion of each of the functional areas. In the lower Mammals this is first seen in the precocious growth of the olfactory cortex and the general cortex as a whole. This results in the formation of a deep rhinal fissure between them. Then the functional areas in the general cortex begin to grow and expand, forming the gyri while their bordering zones lag behind in growth and become the primitive sulci

Hence, the first sulci to appear are those which separate functional areas.

In the higher forms there follows a more complex development. Association fibers invade the periphery of each functional area which thus becomes surrounded by a fringe of gyri and shallow sulci. In this way the original functional areas acquire fringes or the socalled association or psychic areas. In the human brain these fringes become double and somewhat uniform around the visual and auditory areas. Around the sensory and motor areas great irregularities develop out of the special needs of the fore and hind limbs and of the head region. As a final result the primitive limiting sulci come to be far removed from their early positions.

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CHAPTER 8

WHITE SUBSTANCE OF THE CEREBRAL HEMISPHERE

Subcortical plates and furrows, association bundles, corpus callosum, lateral ventricle and internal capsule

UNDERLYING the cortex which is composed of nerve cells and their shorter processes is the white or medullary substance which, on the other hand, is composed of nerve fibers. It is formed by fibers of the internal capsule, corpus callosum and association bundles. The **medullary substance of the gyri and sulci** should be exposed by removing the cortex with a dissector, orange stick or some other suitable instrument, the edge of which is smooth but not sharp enough to cut. It is assumed that the pia has already been pulled off. The work of removal should proceed systematically, following the sulci. Open each sulcus widely to break the cortex at its bottom and with the instrument peel the cortex away from the plate-like medullary substance that forms the center of each of the adjacent gyri. Wash away the shattered cortex. This procedure gives the result seen in figures 45 and 47 in which the large plates of the white substance correspond to the gyri and the furrows to the sulci.

The **subcortical plates** and **furrows** of the white substance are now displayed. Under the sylvian gyri is now seen the insular cortex (64) surrounded by the circular sulcus (75 b). A curved plate of medullary substance (78) enters the sylvian gyri, thickest at their upper end. The ectosylvian gyri (68) are formed over another larger curved plate of the medullary substance. The suprasylvian sulcus (69) is represented by a *C*-shaped furrow that surrounds the sylvian and ectosylvian formations. It is remarkable for its depth, probably due to the overgrowth of the ectosylvian gyri in the Carnivora.

The medullary substance of the suprasylvian gyrus (70) extends forwards (48) and is united with that of the coronal gyrus (38) over an acute bend. Posteriorly it is joined by that of the ectolateral gyrus (50). This formation is very suggestive of the *T*-arrangement formed by the marginal (48), angular (50) and superior temporal (68) gyri in the Primates (fig. 47). The lateral sulcus (41) and the posterior lateral (71) are represented by furrows much shallower than that of the suprasylvian. The medullary center (42) of these gyri forms a long plate that curves over the occipital pole. The anterior end joins the medullary center of the posterior sigmoid gyrus (4).

The furrows for the coronal (1) and ansate (39) sulci are notably deep. They are separated by a thin plate that borders the ansate sulcus and joins with the suprasylvian gyrus. This arrangement is interesting in view of the probable homology of these two sulci with the central sulcus of the Primates. The furrow of the cruciate sulcus (5) forms a deep medium cleft surrounded by the medullary center of the sigmoid gyri (2, 4). Posteriorly this furrow is continued into that of the combined intercalary and splenial sulci. This runs along the medial side of the medullary center of the lateral gyrus (42). Medial to this furrow is a smaller plate of medullary center that radiates into the parasplenial and cingular gyri. This has been removed in figure 46. The medullary center of the frontal region (8) is a large flat plate that invades the frontal and orbital gyri (fig. 45). That which invades the latter is joined to the anterior sylvian so the deep furrow of the presylvian sulcus (3) does not in reality join the rhinal fissure.

The **medullary substance** of the plates and furrows is formed by four sorts of fibers. (1) The **sensory radiations** arise from cells in the thalamus and passing through the internal capsule radiate into the various sensory areas of the cortex. (2) The **motor projection fibers** arise from cells in the motor areas of the cortex and pass down through the internal capsule to form the cerebral peduncles. (3) The **association fibers** constitute the association bundles and form inter-connections between various gyri or areas of the cerebral cortex. These are not much in evidence in the brains of Carnivora but are conspicuous in brains of Primates. (4) The **commissural fibers** constitute the corpus callosum (100) and connect the various cortical areas of the two hemispheres. The corpus callosum is not present in the Monotremata and is definitely added only in orders above the Marsupialia (figs. 23 to 44). The hippocampal (97) and anterior commissures (99) may be included in this fourth group of fibers.

First demonstrate the **cingulum** (fig. 46). Pull away the medullary center from the cingular and parasplenial gyri. A thin layer of fibers joins it to the medullary center of the lateral gyrus and the visual area. Note how this layer is flexed beneath the splenial and intercalary sulci which form a natural boundary between the parasplenial and calcarine areas. Cut the medullary center of the cingular gyrus. As it is drawn backwards a narrow band of fibers, the **cingulum** (*cing*), is seen that turns down back of the corpus callosum to enter the hippocampal gyrus. As it is drawn forwards the cingulum will be found to spread out in the medial surface of the medullary lamina of the frontal gyrus. The cingulum is a constant association fasciculus that appears to connect the hippocampal and parasplenial gyrus with the frontal gyrus.

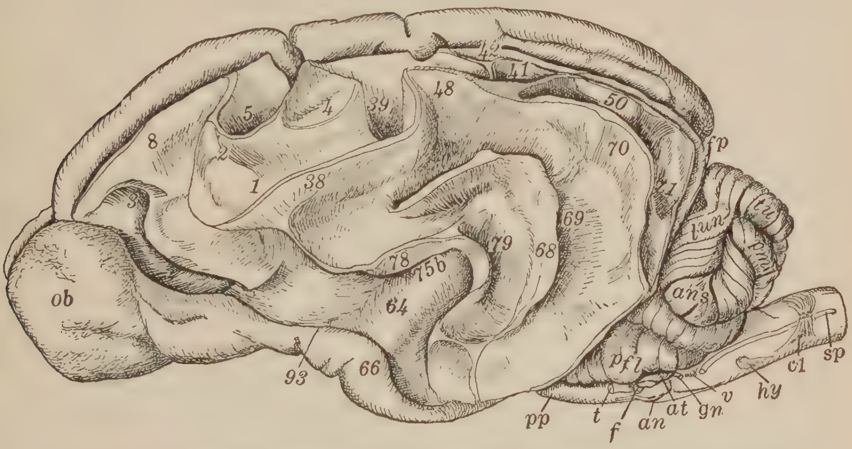

FIG. 45. Medullary substance of left cerebral hemisphere of a dog, × 1⅛. For explanation of numbers see page 26.

The **corpus callosum** (100) can now be displayed by peeling away the medullary center of the lateral gyrus in a lateral direction. The corpus callosum is divided into the medial part or body and an anterior end or genu flexed ventrally towards the terminal lamina, and a posterior end, the splenium, flexed ventrally to join the hippocampal commissure. These relations can be seen best in a median section (figs. 12, 17). The corpus callosum is a great system of commissural fibers that unite the cortices of the two cerebral hemispheres. The fibers of the front end unite the frontal areas. The fibers of the body unite the cortices of the sigmoid, coronal, sylvian, ectosylvian and lateral gyri. The splenium unites the cortices of the occipital region. In the medullary center the fibers of the corpus callosum intersect with those of the internal capsule to enter into the center of the various gyri. Note the two narrow strips of cortex, the **hippocampal rudiment** (98), that curve over the posterior end of the corpus callosum and run forwards near the midline on its dorsal surface.

If the subcortical plates of the sylvian and ectosylvian gyri are stripped away it will be noted that the sylvian gyri receive at their upper end a stalk of fibers from the internal capsule (78); these are the **auditory thalamo-cortical radiations** from the medial geniculate body to the sylvian gyri. At the same time an extensive layer of fibers, the **superior longitudinal fasciculus,** will be found joining the sylvian and ectosylvian gyri with the sigmoid gyri. This appears to form an intimate subcortical connection between these areas. Further dissection reveals a thin layer of gray matter, the claustrum, and a thin layer of fibers, the **external capsule.** This layer of fibers is formed by the **inferior occipito-frontal fasciculus,** that joins the posterior temporal region with the frontal region, in front of the presylvian gyrus. As the layers of fibers in the coronal and parietal regions are stripped away it will become evident that an intimate connection exists between these sensory areas and the sigmoid gyri effected by means of shorter association fasciculi. Beneath the inferior occipito-frontal fasciculus will be seen several blood vessels which pass in on the surface of the **lentiform nucleus.**

The under surface of the corpus callosum lies over the fornix, hippocampus, septum pellucidum and lateral ventricles of which it forms the roof. To demonstrate these relations (fig. 55) carefully cut the corpus callosum lateral to the midline and strip it away laterally, piece by piece. Leave only the front end or genu in position. The lateral ventricle is thus exposed and care should be taken not to injure or disturb the underlying hippocampus and along the midline the hippocampal commissure (*hc* and 97). These are shown in figure 55 after the corpus callosum has been removed. Note as the corpus callosum is removed that, along the midline (fig. 55), it is united to the hippocampal commissure (*hc*) by the septum pellucidum (*sep*) or nuclei septi. Laterally it may be forcibly torn off where it intersects the internal capsule (*int*).

The **subcallosal fasciculus** (*ct*) is another association bundle that will be exposed as the corpus callosum is torn away from the internal capsule. It occurs as a thin sheet of fibers on the ventricular or deep surface of the corpus callosum in the lateral angle of the ventricle. It appears to arise in the visual area that covers the occipital pole and extending forward it extends into the head of the caudate nucleus and the medullary center of the sigmoid cortex that surrounds the crucial sulcus and a more anterior portion is traceable forward into the frontal gyrus. This fasciculus appears to be a direct connection between the visual and frontal areas.

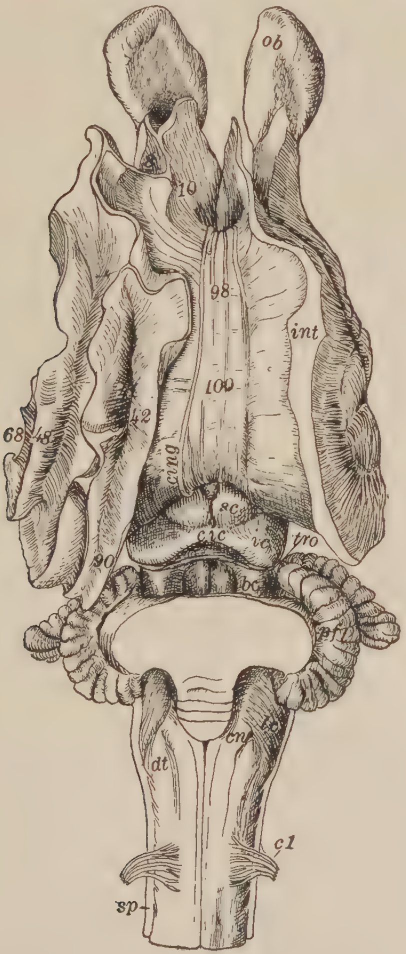

FIG. 46. Medullary substance, corpus callosum and internal capsule of the cerebrum of the dog, × $1\frac{1}{8}$.

The **lateral ventricle** (*lv*) is a large curved space found within the interior of each cerebral hemisphere (fig. 55). In their development the hemispheres originate as hollow vesicles the walls of which are converted into the cortex and medullary substance while the internal spaces remain as the ventricles. They are normally filled with cerebrospinal fluid secreted by the lateral choroid plexuses (*chp*) which protrude into them between the fornix (*fx*) and the thalamus. In the lower mammals the entire space is *C*-shaped curving ventrally around the side of the thalamus so that it may be divided into an anterior or frontal and a posterior or temporal part. In the Primates an extension into the greatly developed occipital pole takes place.

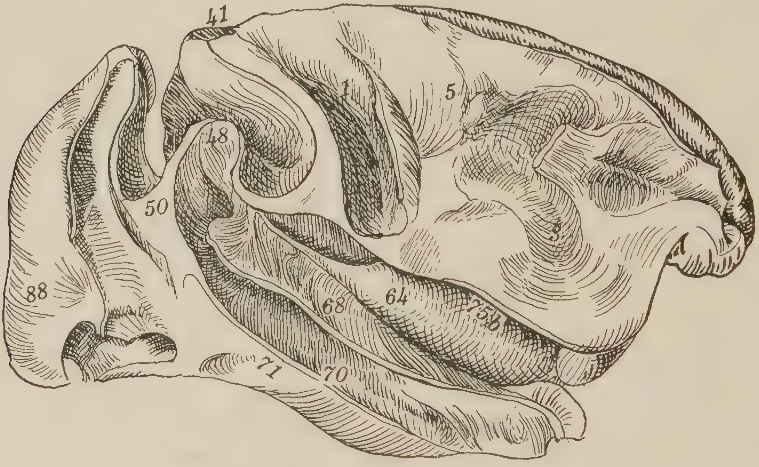

FIG. 47. Medullary substance of cebus capucinus, × 1½. For explanation of numbers see page 27.

Observe that the roof of the ventricle is formed by the corpus callosum which laterally intermeshes with the internal capsule and in front (*cc*) turns down to form the anterior wall of the space. Posteriorly the corpus callosum turns downward over the hippocampus and forms the posterior wall of the space. The medial wall of the space is formed by the septum pellucidum (*sep*) in which appear swellings, the nuclei septi, in the macrosmatic mammals. Posterior to the septum the medial wall is formed by a fusion of the hippocampal commissure (*hc*) with the under surface of the corpus callosum. Posteriorly the floor of the space is formed by the prominent hippocampus (*hip*), fornix (*fx*) and choroid plexus (*chp*) which curve ventrally into the temporal pole. Anteriorly the floor is formed by the head of the caudate nucleus (*cdn*) which continues as a narrow tail parallel to the fornix and choroid plexus into the temporal pole. Behind the nuclei septi and columns of the fornix, the lateral ventricles join the third ventricle through the interventricular foramen.

The **internal capsule** (*int*) is now well defined as a broad *C*-shaped radiation of fibers from the region of the cerebral peduncles and thalamus. Here, as it radiates into the medullary center, it is often called the **corona radiata.** On the lateral side is the cortex of the insula and the medullary lamina of the sylvian and ectosylvian gyri. On the medial side, in the ventricle, is the caudate nucleus (*cdn*) and more posteriorly the choroid plexus (*chp*) and fornix (*fx*) which overlie the thalamus. The internal capsule (*int*) is composed of (1) nerve fibers coming from the thalamus to enter the cortex, that is, afferent thalamocortical fibers and (2) nerve fibers that are leaving the cortex and passing down in the cerebral peduncles as cerebropontal and cerebrospinal fiber tracts. These systems of fibers constitute the chief afferent and efferent connections for the cerebral cortex; hence the great importance that is assigned to the internal capsule. The entire *C*-shaped fan of the internal capsule (fig. 46) may be divided into the frontal part which radiates into the cortex of the frontal region (10), the middle part which radiates into the gyri of the parietal and suprasylvian region (42 and 48), and occipital part which radiates into the occipital region (90) and a ventral temporal part which radiates into the temporal region (68).

The **thalamo-cortical radiations** are systems of fibers that arise in the various nuclei of the thalamus and pass into the cortex and conduct into it the various sensory excitations. As they enter the internal capsule they are the medial constituent of it. The **auditory** thalamo-cortical **radiations** arise from the medial geniculate body, pass through the temporal part of the internal capsule to reach the cortex of the posterior sylvian and transverse temporal gyrus. The **optic radiations** (*or*) arise in the lateral geniculate body and pulvinar and pass through the occipital part of the internal capsule to reach the cortex of the calcarine fissure and lingual gyrus. The kinesthetic or deep sensibility radiations (*sr*) arise from the lateral nucleus of the thalamus and reach the coronal and postcruciate cortex or postcentral gyri. A number of other radiations leave the thalamus but their cortical distribution is not well known.

For a description of the **projection fibers** that leave the cortex, see page 126. They form the lateral constituent of the internal capsule and enter into the formation of the cerebral peduncles.

The human brain has always furnished a ready means for demonstrating the various components of the medullary centers (fig. 48). As the cortex is pulled off note the course of the **short association fibers** connecting adjacent convolutions. Identify then the **sensory radiations** (*sr*) that enter the postcentral gyrus (38 and 40) and a parallel series of fibers, the **cerebrospinal tracts** (*cs*), that enter the precentral gyrus. The **auditory radiations** (*ar*) enter the transverse temporal gyrus, and like it, are often double. A large leaf of fibers enters the inferior parietal and frontal gyri. When this is broken off there will be found running through its base the large **superior longitudinal fasciculus** (*slf*). This is a bundle of great importance highly developed in the human brain. It connects the angular (50), parieto-occipital (52), middle temporal (70) and inferior parietal gyri forward with the inferior and middle frontal gyri. In its course it crosses through the lower part of the sensory radiations (*sr*) and the cerebrospinal tracts (*cs*) which are broken off in the figure.

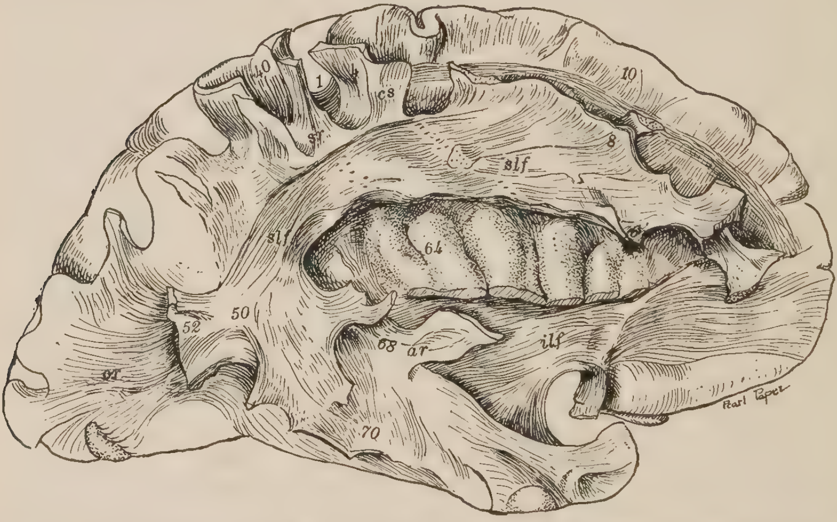

FIG. 48. Association bundles in the human brain, × ⅔. *slf*, superior longitudinal fasciculus; *ilf*, inferior longitudinal fasciculus; *or*, optic radiations; *ar*, auditory radiations.

When the posterior end of this bundle that radiates into the parieto-occipital gyrus (52) is raised, there will be found beneath it a large band of fibers, the **optic radiations** (*or*) that surround the occipital horn of the lateral ventricle and enter the cuneus and lingual gyrus.

Beneath the lower half of the island (64) will be found the **inferior longitudinal fasciculus** (*ilf*) which connects the inferior temporal cortex with the inferior frontal and orbital cortex.

On the medial surface, the **cingulum** can be demonstrated to connect the region of the precuneus with the superior frontal gyrus. When these are removed the distribution of the corpus callosum can be seen. Where it interdigitates with the thalamo-cortical radiations there will be found, though deeply situated, the **superior occipito-frontal fasciculus.** On the ventricular surface it forms the primitive **subcallosal bundle** (*ct*) which spreads over the head of the caudate nucleus.

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CHAPTER 9

THE OLFACTORY BRAIN OF MAMMALS

THE olfactory brain is the primitive forebrain common to all true vertebrates. It is the organ of smell connected with the olfactory membranes in the nasal sacs or in the nose by means of the olfactory nerves. The three stages in its evolution are briefly indicated.

In Cyclotomes, Fishes and larval Amphibia the organization of the forebrain is the most primitive. Its function of smell depends upon the response of this organ to sapid (organic) substances in solution in water in which the animal lives. And its chief use is in connection with the selection of food. The evolution of the primitive water smelling or aquasmatic brain will be outlined in chapter 40.

In adult Amphibia and the Reptiles the nasal sacs were subjected to the unfavorable drying effects of the atmosphere which greatly reduced the functional value of the primitive water smelling forebrain. Devices such as the vomero-nasal organ, and the amygdalar complex were early developed to cope with this unfavorable situation. A more complex development followed by which the olfactory organ was adapted for the reception of infinitely dilute volatile substances in air. This was made possible by the development of the hippocampal formation and the pyriform cortex for the intensification of these minute olfactory stimuli.

The important stage of olfactory development came in the Mammals. With the formation of highly convoluted turbinate bones in the nasal cavities, closely arranged for the maintenance of a moist surface, the olfactory mucous membrane and the olfactory nerves and bulbs became greatly enlarged. Thus at the lower level of the mammals we find the olfactory brain large or macrosmatic, fully adapted to terrestrial life The olfactory membrane is greatly expanded over a new system of convoluted turbinate bones, protected in nasal cavities, always moist and highly sensitive to weak smells. The pyriform and hippocampal cortices are greatly expanded and the amygdalar centers are fully retained. Thus there is created in the lower mammals an elaborate mechanism for the reception, dissemination and intensification of the impulses arising from minute olfactory stimuli. This kind of nervous function may be spoken of as **irradiation** to distinguish it from reflex tonic and inhibitory activities such as are inherent in the spinal cord, brain-stem, cerebellum and the primitive forebrain. This function of irradiation depends upon a large expanse of cortex composed of nerve cells of low irritability standing in intimate connection with each other in all directions. Out of the dorsal wall of this olfactory brain there finally arose the cerebral cortex, a great cellular mantle irradiated by receptive fibers from organs other than smell, such as the retinae (vision), the cochlea (hearing), the muscle spindles (deep sensibility), the cutaneous receptors (surface sensibility) and the taste buds.

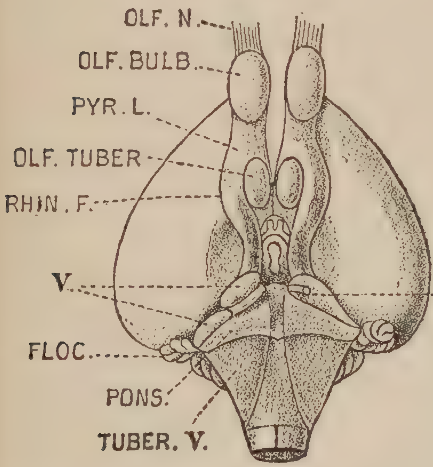

Fig. 49. Brain of duckbilled platypus, ventral view, × 1⅓.

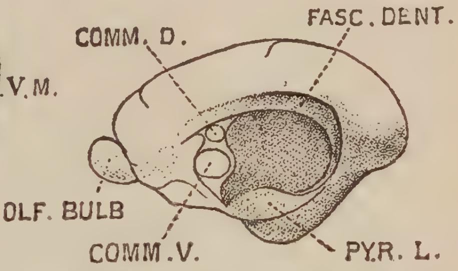

Fig. 50. Cerebrum of duckbilled platypus, medial view of right half, × 1⅓.

From G. E. Smith.

Olfactory brain of Monotremes and Marsupials

In the lowest mammals, the Monotremes, as shown by the brain of the duck-billed platypus (*ornithorhyncus anatinus*, figs. 49 to 51) the entire forebrain is primitive. The cerebral hemispheres are well developed though no sulci or gyri are apparent on their surfaces (fig. 1) to indicate the beginning of functional subdivision. On the ventral and medial side of each hemisphere is seen the **olfactory brain.** In front, under the frontal pole of the cerebrum is the oval **olfactory bulb** (*olf. bulb*). Filaments of the olfactory nerves (*olf. n.*) enter the frontal end of the bulbs, an arrangement commonly found in fishes and reptiles, but not in other mammals. The semiaquatic life of this animal and its elongated duck-like bill must be recalled in this connection. The posterior end of the bulb is connected by a broad olfactory stalk with a small but prominent olfactory tubercle (*olf. tuber*) and a narrow, much reduced band

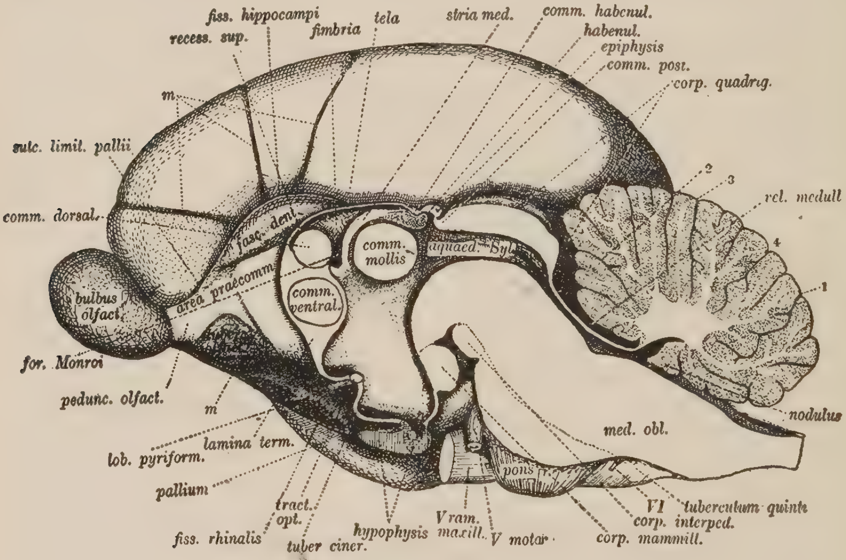

FIG. 51. Brain of duckbilled platypus, medial view, × 3. After G. E. Smith.

of cortex, the **pyriform area** (*pyr. l.*). This is separated on the lateral side from the cerebrum by a deep **rhinal fissure** (*rhin. f.*). Between the pyriform lobe and the olfactory tubercle a deep **endorhinal fissure** is present. This is peculiar to Monotremes. The fibers that connect the bulb with the pyriform area are scattered and do not form a compact tract as they do in other mammals. The condition in this monotreme resembles that of reptiles.

On the medial surface (fig. 50) the posterior end of the pyriform area is seen to pass laterally into the **dentate gyrus** (*fasc. dent.*). This gyrus curves dorsally and forwards over the thalamus (which in the figure is partly cut away) to join the cortex in front of the two commissures. The fiber band that passes along the ventral edge of the dentate gyrus is the fornix. And the deep cleft, the hippocampal fissure, separates it from the surrounding cortex which may be designated as the hippocampal gyrus. The two commissures above the terminal lamina are the **anterior commissure** (*comm. v.*) below, and the **hippocampal commissure** (*comm. d.*) above. No corpus callosum nor cerebral commissure is evident. Particular attention should be given to the fact that the dentate gyrus, which indicates the extent of the hippocampal formation on the ventricular surface, forms in this lowest of mammals almost a complete ring around the thalamus, uniting by its two ends the pyriform area with the precommissural area (fig. 51). For a systematic study in the various orders of mammals of the hippocampal and precommissural areas, the commissures and the evolution of the corpus callosum, the reader is referred to the exhaustive studies of G. Elliot Smith (especially the Catalogue of Brains in the Museums of the Royal College of Surgeons of England, volume 2 of the Physiological series).

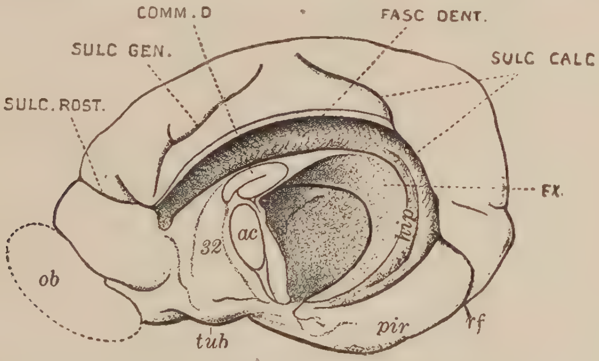

FIG. 52. Cerebum of kangaroo, medial view of right half, × 1⅛.
From G. E. Smith.

The Marsupials present a well-developed olfactory brain. A medial view of a cerebral hemisphere of the black-faced giant kangaroo (*macropus giganteus*) is shown in figure 52. It will be seen that in this mammal (a marsupial) the olfactory bulbs and secondary centers are large. This is a **macrosmatic** or large smell brain, typical of all of the lower terrestrial mammals, associated with a complex system of turbinated bones covered by a greatly expanded olfactory mucous membrane. A comparison of this macrosmatic olfactory brain with the lowly developed forebrain of the platypus (figs. 49, 50) will at once reveal the great advance in cerebral organization that the macrosmatic conditions have made possible. The rhinal (*rf*) and hippocampal fissures indicate a distinct separation of the olfactory cortex (*pir, hip*) from the somatic cortex.

The olfactory brain of Rodents, Carnivora and Primates

The olfactory brain of Insectivora, Rodents, Ungulates and Carnivora is macrosmatic and the various parts can readily be studied on properly cleaned and dissected specimens. In making this study compare the specimens with figures 9, 55, 73 and 74.

The rabbit (a rodent, fig. 9) brain provides a good example of a macrosmatic brain with a very lowly developed cerebral cortex and corpus callosum. The brain of a cat (fig. 73) or a dog (fig. 74), though still macrosmatic, has a well-developed cerebrum with several well-defined functional areas. Primates, chiefly on account of their arboreal and anthropoid habits, have come to depend upon the eyes, ears and general sensibilities and the formation of new associations of these sensibilities in their cortex. As a result their olfactory brain has become reduced in functional importance and has suffered an actual reduction in most of its parts. Such brains are called microsmatic. With the exception of the low terrestrial lemur, chiromys (*aye-aye*), the lemurs, marmosets, monkeys, baboons and anthropoid apes (all included as Primates) possess microsmatic brains which in all details correspond to the fundamental mammalian plan. Therefore, a single description will be given to cover all of the orders.

On the ventral surface of the brains are found the **olfactory bulbs** (12 or *ob*). Note how much larger they are in the lower macrosmatic mammals (rabbit, cat, dog). The bulbs lie on the cribriform plate of the ethmoid bone and receive through its foramina the numerous filaments of the olfactory nerves. When the nasal chamber of one of these animals is opened by means of a midline cut, an elaborate system of turbinated processes is seen, covered over by a moist olfactory mucous membrane. The olfactory nerve is also very elaborate, consisting of a large number of filaments which enter the surface of the olfactory bulb. The usual fuzzy appearance of this is due to the tearing away of the olfactory fibers. Crossing the medial surface of the bulb a special accessory olfactory or **vomero-nasal nerve** will be seen which ends in the dorsomedial side of the bulb near its posterior limit in a small depressed area known as the accessory olfactory bulb. Since the vomero-nasal organ which this nerve supplies is rudimentary in mammals, the nerve and its centers are also rudimentary. In the microsmatic primates the bulbs are reduced in size.

The bulbs are connected with the frontal and basal portion of the brain by the olfactory stalk in which will be seen the **olfactory tracts** or stria appearing as white strands. In the lower mammals the olfactory stalk is a tubular structure containing in its center a hollow cavity. In the Primate brain this cavity is obliterated during development. Where the olfactory stalk joins the brain there appear the **olfactory triangle** (34) and the **olfactory tubercle** (36 or *tub*). In the Primate brain they are small and hard to recognize, but in the brains of the macrosmatic mammals they are large. Note how the tubercle spreads posteriorly to the **diagonal band** (*db*). If a section of the brain is made through this level

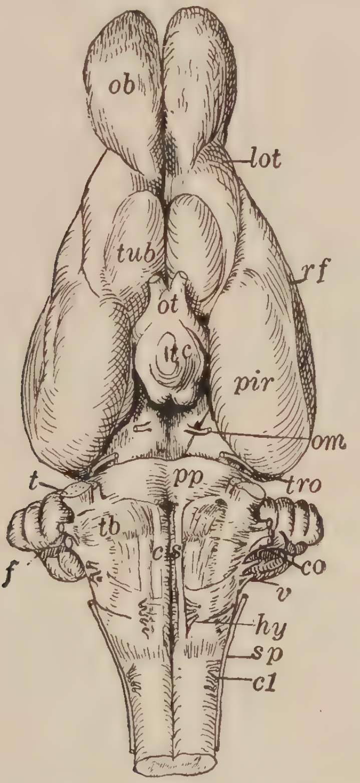

FIG. 53. Brain of opossum, ventral view, × 2.
For meaning of letters see page xxi.

(fig. 176) it will be seen that this area is spread over the inferior surface of the head of the **caudate nucleus.** The perforations in it are due to an unevenness of the cortex and to the numerous small vessels that have been pulled out with the pia. Note on the lower animal brains (figs. 73 and 74) along the lateral border of the olfactory stalk, the anterior part of the pyriform area (66) or limen insulae in the Primates. This is a band of cortex that runs from the lateral part of the olfactory stalk posteriorly and laterally to the pyriform area (66 or *pir*), which covers the tip of the temporal lobe. The white band passing from the olfactory bulb to the medial border of the pyriform area is the **lateral olfactory tract** or stria (*lot*). Note the **rhinal sulcus** (93 or *rf*) that separates the pyriform area from the general cerebral cortex. It is always distinct in the lower mammals and at its bottom the cortex of the pyriform area is united with the insula. In the Primate brain the sulcus is effaced during development, by the great lateral expansion of the brain.

Most of the lateral olfactory tract (*lot*) is lost in the medial border of the pyriform area. A part of it ends in the small lateral olfactory tubercle in front of the posterior pyriform area. The diagonal band of Broca is a flat band-like area (*db*) extending from the lateral olfactory tubercle in front of the optic tract (*ot*) and behind the olfactory tubercle (*tub*). Above the optic chiasma at the midline it turns onto the medial surface and becomes the subcallosal gyrus (32).

Many small strands of fibers from the olfactory bulb can be seen entering the region of the olfactory tubercle (*tub*). A small band, the medial olfactory tract, covered by cortex, turns from the olfactory triangle onto the medial surface into the region of the parolfactory gyrus (30) and the gyrus subcallosus or precommisural area (32).

The **pyriform area** (*pir*) which spreads over the tip of the temporal lobe is clearly seen on the inferior and lateral surfaces in brains of lower mammals but in the human brain it is sharply bent forward over the limen insulae and forms the greater part of the pyriform hook. It can be seen best on the Primate brains when a portion of the thalamus has been cut away as in figures 24 to 44. This great bend has been produced by growth of the corpus callosum and forward crowding of the temporal lobe. The hippocampus and dentate gyrus have likewise been drawn forward and flexed, forming the hook or **uncus** (94). In the duckbill (fig. 50), kangaroo (fig. 52) and the rabbit note that these flexures have not occurred. In the cat and dog a partial flexure has taken place. In the Primate brain this flexure is complete and the formation of the uncus is fully realized. Moreover the amygdalar elevation (*amy*) which is seen on the ventral surface in the lower mammals is to be looked for on the dorsal surface of the temporal pole in the Primates due to a medial rotation of the pyriform area.

For the study of the hippocampal formation, two kinds of preparations are needed. Medial views of the brains (figs. 6, 77) in which a portion of the thalamus has been cut out, show the hippocampal formation and fornix to good advantage. (See figures of medial views of primate brains, 24 to 44.) A human brain is especially good for this purpose. Such specimens in which the corpus callosum has been removed show the ventricular surface of the hippocampal formation, the fornix and the nuclei septi. Examine such a preparation first.

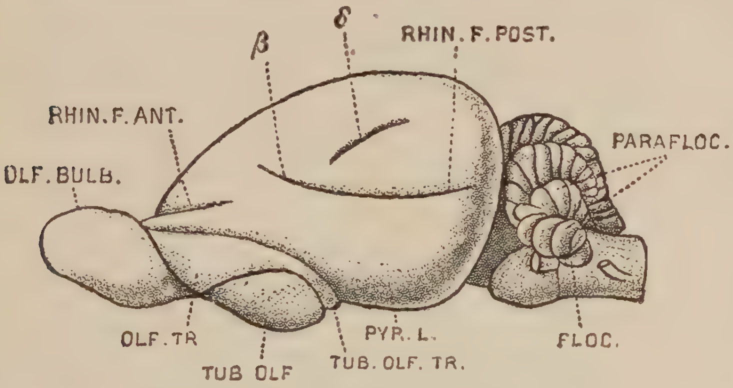

Fig. 54. Brain of armadillo, lateral view, × 1½.
After G. E. Smith.

The **hippocampus** (*hip*) is a deeply buried gyrus which forms a prominent curved elevation in the ventricular surface (fig. 55). The inner surface of the hippocampus is covered by a layer of white nerve fibers which unite along its inner edge to form the fornix (95 or *fx*). The fornix also forms the medial margin of the cerebral hemisphere and curves freely beneath the corpus callosum (100 or *cc*) over the thalamus (101) to sink into its medial wall and enter the mammillary body (*mb*) on the ventral surface of the brain. Many of its fibers cross under the posterior part of the corpus callosum (which has been removed) to form the **hippocampal com-**

missure (97 or *hc*). Though the fornix curves freely over the thalamus the two structures are united by a thin membrane which is protruded into the lateral ventricle to form the lateral **choroid plexus** (*chp*). Hence, this potential cleft between the thalamus and the fornix is known as the choroid fissure.

As the corpus callosum buckles dorsally in the higher mammals (this can be seen best in a medial view) its anterior end is drawn away from the fornix. The two lamina that connect its under surface with the two fornices are the septum pellucidum (*sep*). They represent cortex that appears to have been drawn in from the region of the preterminal area or subcallosal gyrus (32) in the formation of the corpus callosum. In the macrosmatic mammals (fig. 53) large **nuclei septi** (*sep*) occur in the septum on each side in front of the fornix.

The fornix (*fx*) on one side may now be cut just back of the nuclei septi and the hippocampal commissure may be cut along the midline as in figures 75 and 76. As the fornix and hippocampal formation are raised away in a backward direction the choroid plexus is seen to be joined to the velum interpositum. This velum is a layer of pia interposed between the thalamus and hippocampal formation. The line along which the plexus is torn away from the fornix is the tenia fornicis. The hippocampal formation and velum cover over the thalamus. The line along which the plexus is attached to the thalamus is the tenia thalami. Note how the plexus and its teniae circle around back of the thalamus into the tip of the temporal pole.

The hippocampal gyrus and the dentate gyrus should now be examined on the under surface of the hippocampus. In this connection examine also a specimen in which the thalamus has been partly removed to show the hippocampal formations from the medial side.

The hippocampal gyrus (104) is an external band of cortex along the medial margin of the temporal lobe (figs. 28 to 44), fringed by the **dentate gyrus** (96). It is continuous below with the cortex of the pyriform area (66 or *pir*) and laterally with the hippocampo-fusiform gyrus (82), posteriorly with the lingual gyrus (84) and behind the corpus callosum with the parasplenial gyrus (62). However, in the Carnivora and Ungulata the deep anterior calcarine sulcus (85) separates it almost completely from the adjacent gyri. The surface of the hippocampal gyrus is covered by a thin stratum of fibers which impart to it a white appearance. These arise in the pyriform area and enter the hippocampus.

Along the inner or lateral border of the hippocampal gyrus occurs the deep cleft or **hippocampal fissure,** occupied by the **dentate gyrus** (96) which receives its name from the tooth-like appearance of its surface in brains of Primates. Lateral to it, is often seen a narrow strip of the hippocampus lying next to the fornix. In the ordinary specimen, the hippocampus itself is an inturned gyrus so completely hidden from view that only a section through this

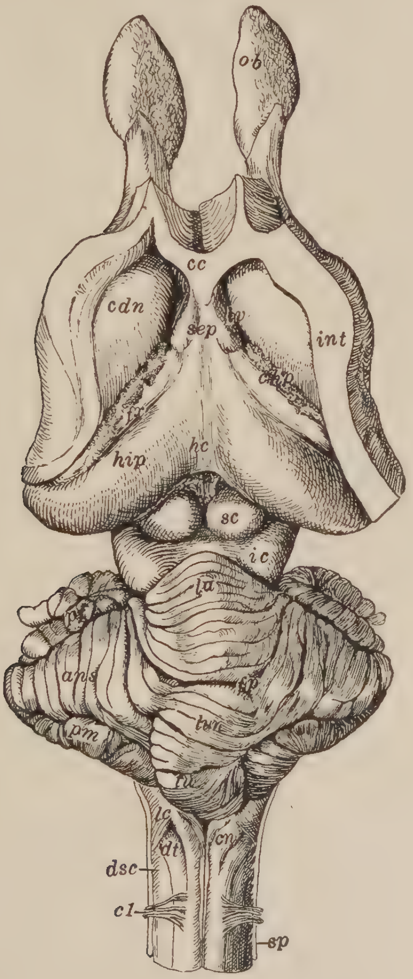

Fig. 55. Brain stem of a dog, showing hippocampus exposed by removal of the cerebrum, dorsal view, × 1⅛.

region will reveal it. It forms the prominent bulging seen on the ventricular surface.

As you examine the dog brain (fig. 55) two white bands are seen medial to the dentate gyrus and hippocampus. The medial one is the hippocampal commissure (*hc*). The lateral one is the fornix (*fx*). How the fornix must pass through the medial wall of the thalamus to reach the mammillary body can be best seen in a median section.

In the temporal pole both hippocampus and dentate gyrus are flexed to form the uncus (94). Under the posterior end of the splenium of the corpus callosum the hippocampus departs from the fornix and turns back over the corpus callosum to form the hippocampal rudiment. The primitive position of the hippocampus dorsal to the commissures and the relation of its front end to the preterminal area can be seen in the brain of the kangaroo (fig. 52). In the rabbit (fig. 6) the dorsal end of the hippocampus is pushed further back by the still small corpus callosum (*cc*). In the Carnivora, Ungulata and Primates this expansion of the corpus callosum and the backward migration of the dorsal end of the hippocampus become extreme. But on the dorsal surface of the corpus callosum there remains a narrow ridge on each side of the midline which is called the longitudinal stria, or more appropriately, the hippocampal rudiment.

In front of the **anterior commissure** (*ac*) and below the front end of the corpus callosum (*cc*) is seen the subcallosal gyrus or preterminal area (32). Its connection with the origin of the septum pellucidum (*sep*) has been mentioned. If the gyrus subcallosus is traced laterally above the chiasma it will be seen to continue into the diagonal band of Broca (*db*). In front of the gyrus subcallosus is the parolfactory gyrus (32). The medial olfactory tract ends in this region. In macrosmatic brains such as that of the dog the extent of the olfactory tubercle and diagonal band onto the medial surface is clearly shown. How the preterminal area which they form extends in front of the terminal lamina and anterior commissure and extends under the anterior end of the corpus callosum into the region of the septum pellucidum (nuclei septi) is well seen in the rabbit (fig. 6).

The **amygdalar nucleus** (*amy*) is situated in the tip of the pyriform area (fig. 9) beneath its cortex. How it has been turned over so that its ventral position in the lower orders is changed to a dorsal concealed position in the Primates has already been explained as due to the forward flexion and the medial rotation of the pyriform lobe. A narrow band of fibers (fig. 78), the **terminal stria** (*tst*), is seen to arise from the amygdala. On the ventricular surface the stria passes in the groove between the thalamus and caudate nucleus forward in the manner of the fornix, and like the fornix, it disappears by plunging ventrally in front of the thalamus. Its termination is in the large nuclear mass that forms the olfactory tubercle on the ventral side of the brain.

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CHAPTER 10

THE CEREBELLUM OF MAMMALS

NEXT to the cerebral hemispheres, the cerebellum, or small brain, is the most highly elaborated organ of the brain. Like the former it is distinguished by the presence on its surface of a cortex or a gray mantle of nerve cells. This cortex is spread in the form of narrow leaf-like gyri or folia over a central tree-like arrangement of white nerve fibers. A glance at the cerebellum of any common mammal (fig. 63) will show the narrow ridge-like arrangement of the folia and their tendency to extend in a transverse direction. A vertical section through the cerebellum (fig. 67) shows that the folia are shallow out-foldings and that only a small number are visible on the surface, many being hidden and forming the walls of deeper clefts called fissures and sulci.

In such a section the white, central, tree-like expanse of nerve fibers can be followed to every folium and one can understand how the cells that constitute the cerebellar cortex can be connected by means of the nerve fibers in this white layer with distant parts of the brain. This becomes more evident when the white layer is traced to the base of the cerebellum where it is seen to form on each side the three cerebellar brachia or stalks (fig. 72) which unite it with the medulla, pons and midbrain. Now if one examines a cerebellum cut across the middle of its lateral lobes (fig. 147) there will be seen in the core of the white matter, gray masses of cells, the cerebellar nuclei, which stand in particular relation to the brachium conjunctivum though surrounded by the other two.

The histological structure of any part of the cortex (fig. 154) reveals a peculiar arrangement of cells common to all parts but totally unlike anything in the cerebral cortex or elsewhere in the nervous system. Three layers are evident, (1) a thick layer of granule cells (*G*) surrounding the white matter, (2) a layer of giant Purkinje cells (*Pc*) on the surface of the granule layer, (3) a surface molecular layer (*M*) consisting of an intricate brush-like interrelation between fibers that radiate into it from the white substance, the granular layer and the Purkinje cells.

The cerebellum of the marsupial mole (notoryctes t.)

"The simplest mammalian cerebellum, that of the small marsupial mole (notoryctes typhlops, Stirling), represents a stage through which the more complex organ of all other mammals passes at an early stage in its developmental history. This organ with its fully developed histological structure affords a very useful demonstration of the fundamental plan of the mammalian cerebellum. That the cerebellum of notoryctes is really a primitive (and not a retrograde) type is shown by its close resemblance to that of perameles, the most generalized mammal known to us; but by reason of its much smaller size the cerebellum of notoryctes is much simpler even than that of perameles and lends itself better to histological investigations. Wherefore, in taking notoryctes and perameles as our basal types we are dealing with undoubtedly primitive forms." (G. Elliot Smith.)

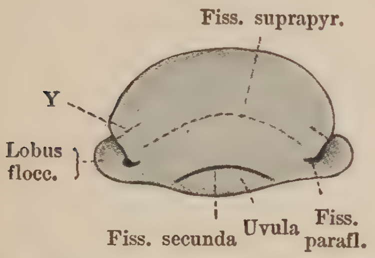

FIG. 56. Cerebellum of notoryctes, posterior view, × 4.

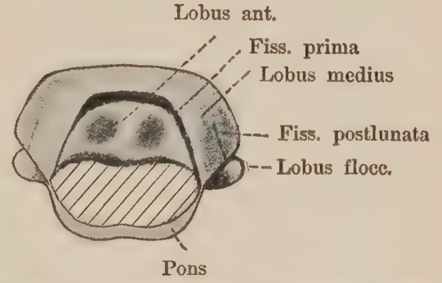

FIG. 57. Cerebellum of marsupial mole, notoryctes, anterior view, × 4.

From G. E. Smith.

The cerebellum of notoryctes (figs. 56 and 57) is oval in shape, possessing on each side of its base a small appendage, the **floccular lobe.** Its anterior surface shows two shallow impressions where it lies pressed against the inferior colliculi of the mid-brain. A deep semilunar cleft, the **fissura prima** (preclival fissure) cuts off a small **anterior lobe** from the **middle lobe.** The depth and fundamental nature of this fissure (*fp.*) can be seen in the sagittal section (fig. 58). Its significance is probably functional as well as morphological. No folia or other subdivisions are visible in the surface of the anterior lobe. On the posterior surface the **fissure secunda** (*fs.*) or postuvular or prepyramidal fissure cuts the mid-line and separates the large middle lobe (*lm.*) from the **uvula** (*uv.*) and **nodulus** (*no.*). The latter two are separated from each other by a **postnodular fissure.**

Together they constitute the posterior lobe. Laterally a narrow connection unites them with the laterally placed **floccular lobe.** A shallow groove divides the floccular lobe into an upper and a lower segment. These are the forerunners of the **paraflocculus** and **flocculus** of higher forms.

The middle lobe is the largest area of the cortex and surrounds the anterior lobe like a hood. Behind the fissura prima each side of the surface of the middle lobe is cut by a shallow postlunate or postclival fissure (fig. 57). This indicates the beginning subdivision into the **lunate,** simple or clival lobule in front and the **ansiform** or semilunar lobule behind it. It is probably due to the growth (expansion) of the ansiform lobule and to a difference in functional connections of the two lobes. The manner in which the middle lobe forms a hood over the anterior lobe can be seen in the sagittal section (fig. 58).

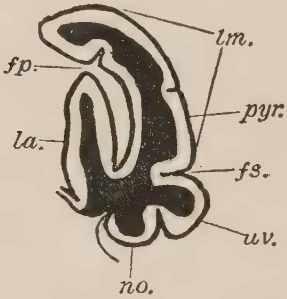

FIG. 58. Medial section of cerebellum of notoryctes, × 4.

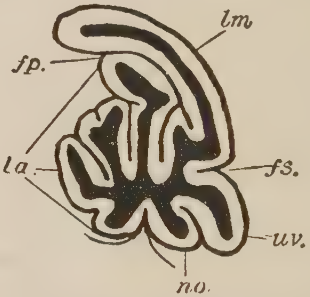

FIG. 59. Medial section of the cerebellum of perameles, × 4.

The anterior surface of the lunate lobe that forms the posterior wall of the fissura prima exhibits a single wrinkle under the margin of the fissure, possibly a folium. It should be noted that the ansiform and lunate lobules in this cerebellum are nothing more than the lateral expansions of a common middle lobe with no indication of the separation between the median and lateral parts such as is seen in more developed cerebella of higher mammals. A shallow but often complete **suprapyramidal fissure** is seen on the posterior surface (fig. 56) separating the **pyramis** from the middle lobe. The **pyramis** is seen to extend laterally towards the flocculus. The posterior side of each lateral lobe is cut by a shallow inconstant furrow, probably the **postansiform fissure** of higher forms. This indicates an early stage in the separation of the ansiform (semilunar) lobule from the area behind it which with the lateral extensions of the pyramis will form the **paramedian lobe** of more highly differentiated cerebella.

The primitive plan of subdivision which is presented by the simple cerebellum of notoryctes has been shown to prevail among the mammals. A median section of the cerebellum of perameles, the bandicoot (fig. 59), reveals a fissura prima (*fp.*) and fissura secunda (*fs.*) separating the anterior and posterior lobes from the middle lobe. The anterior lobe (*la.*) is now separated into four lobules by three transverse sulci and there are indications of folia on the surface of the two dorsal lobules. The posterior lobe consists of the median nodulus (*no.*) and uvula (*uv.*) connected laterally with the prominent floccular lobe. The middle lobe (*lm.*) is still simple and comparable with that of notoryctes.

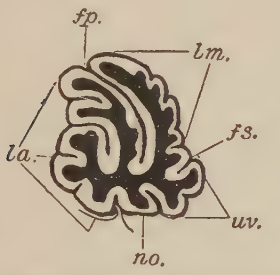

FIG. 60. Medial section of the cerebellum of a hedgehog, × 4.

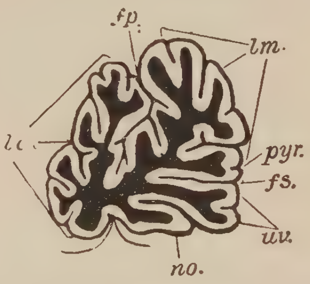

FIG. 61. Medial section of the cerebellum of a lemur, × 4.

From G. E. Smith.

The cerebellum of the rabbit

The rabbit cerebellum (figs. 6 to 9) shows the cerebellum subdivided by the **fissura prima** (*fp*) into an **anterior lobe** (*la*) and a **middle lobe** or tuber (*tu*). The fissure appears early in fetal development, on the 21st day. The anterior lobe (*la*) is further subdivided into three lobules, each covered with a number of folia totalling about 14. A **postlunate fissure** separates a *U*-shaped **lunate lobule** (*lun*) from the **ansiform** or **semilunar lobule** (*ans*) on each side. Each of the lunate lobules consists of two folia connected by a single folium, uppermost over the mid-line. The ansiform lobules (*ans*) consist of four folia projected laterally behind the lunate lobules. Behind the folium that connects the lunate lobules, the cerebellar cortex shows a pronounced separation into the lateral **paramedian lobules** (*pm*) with five folia and a median **tuber vermis** (*tu*) with several folia separated by a medullary area devoid of a cortex which becomes the **paramedian sulcus** in higher forms. The **paramedian lobule** projects at the upper border of the cerebellum and a definite **postsemilunar** (or postansiform) **fissure** (*pa*) separates it from the ansiform lobule. Below the tuber vermis is a large median **pyramis** (*pyr*) consisting of two or more large folia which extend laterally to join the **paraflocculus** (*pfl*). A deep **parafloccular fissure** separates the paraflocculus from the paramedian lobule. The paraflocculus extends forward and laterally and forms a semicircle of about ten folia (the petrosal lobe). Below it, is the small **flocculus** (*fl*) consisting of about four folia connected by a very narrow strand with the median **nodulus** (*no*) and **uvula** (*uv*). The latter two constitute the posterior lobe and are separated from the pyramis by the **fissura secunda** (*fs*), prepyramidal or uvular fissure.

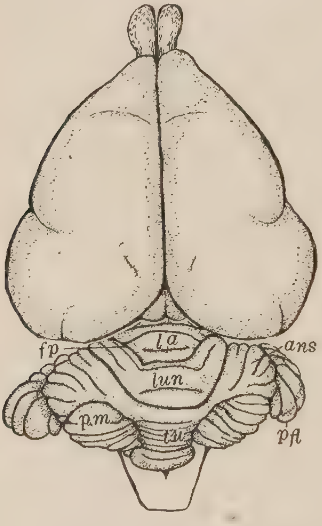

FIG. 62. Brain of a marmot, woodchuck, dorsal view, × 1½.

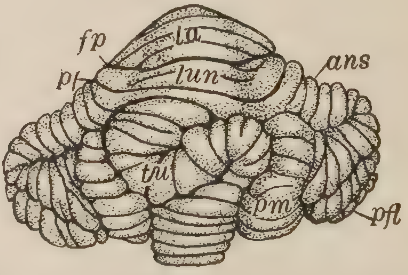

FIG. 63. Cerebellum of a cat, dorsal view, × 2.

The cerebella of higher mammals

If now a comparison of cerebella in an ascending series of mammals such as marmot, cat, dog, cebus, baboon and a human babe is made it will be seen that the cerebellum is naturally divided into anterior, middle, posterior and floccular lobes (figs. 62–71). The anterior (*la*) and posterior lobes (*uv*) are median structures; the floccular lobes (*pfl*) are bilateral; while the middle lobe is median (*tu*) as well as bilateral (*ans*, *pm*). As the number and complexity of cerebellar folia is increased the lobes are further subdivided into lobules. The lobes and lobules indicate a territorial subdivision of the cerebellar cortex which has a functional as well as morphological meaning. For meaning of letters on figures see page xxi.

In all these animals the **anterior lobe** (*la*) is defined by the **fissura prima** (*fp*) or preclival fissure which separates it from the lunate lobules (*lun*) of the middle lobe. In a median section (figs. 6, 60, 61, 67) this fissure (*fp*) is readily identified, and the further subdivision of the anterior lobe (*la*) into the small ventral lingula, the alar and the large culminate lobules shows the prevailing arrangement of lobules. The anterior lobe is seen to be a median structure (rabbit, marmot, cat) in the lower mammals such as the Rodents, Ungulates and Carnivora. In the dog (fig. 55) a lateral spreading of the lobe (*la*) is recognizable, in lemurs it becomes evident and in monkeys and apes and man (figs. 68 to 70) it is a prominent feature. Though this lateral expansion is pronounced in the Primates it cannot be said that there is any definite subdivision of the anterior lobe into a median **vermis** and **lateral lobes** such as is found in the middle lobe behind the fissura prima.

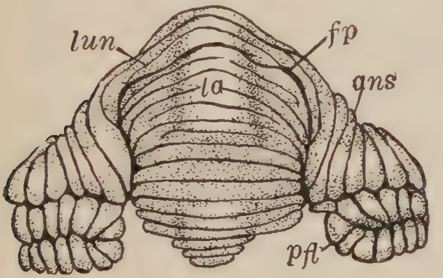

Fig. 64. Cerebellum of a cat, anterior view, × 2.

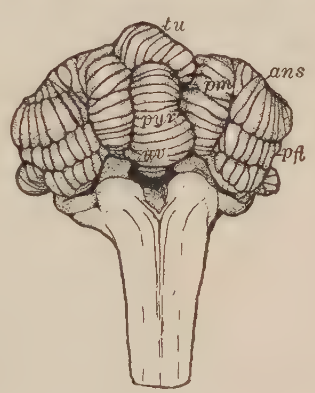

Fig. 65. Cerebellum of a cat, posterior view, × 1½.

The **posterior lobe** consists of two lobules, the **nodulus** (*no*) and **uvula** (*uv*), limited to the mid-line or vermis. Throughout the mammalian orders it remains relatively small with no tendency to a lateral expansion such as is manifested by the anterior lobe in Primates. Of the two lobules, the uvula is the larger. The nodulus remains small but is connected laterally with the **flocculus** (*fl*) by means of a curved white band, the peduncle of the flocculus (fig. 66, *pf*). Along this peduncle a narrow band of cortex is often seen connecting the nodulus with the flocculus (*fl*). The peduncle forms the natural posterior inferior boundary of the lateral halves of the cerebellum. As it extends across the posterior surface of the upturned restiform body it gives attachment to the posterior medullary velum. The postnodular sulcus separates the nodulus from the uvula. The uvular or prepyramidal sulcus (*fs*) separates the uvula from the pyramis and on account of its early appearance and morphological importance is also called fissura secunda.

The **floccular lobe** (*pfl*) is bilateral and consists of two lobules, the flocculus and paraflocculus. The **flocculus** (*fl*) is a small cluster of folia ventral to the paraflocculus on the lateral surface of the restiform body (*rb*) but connected over the back of this with the nodulus by means of the peduncle of the flocculus. The flocculus maintains its relative size throughout the mammals. The **paraflocculus** (*pfl*) consists of a long loop of short folia whose two parallel limbs extend across the outside of the cerebellar peduncles between the flocculus and the lateral lobe. The ventral limb joins the flocculus along its peduncle. The dorsal limb joins the pyramis in the lower mammals by a connection known as the copula pyramis as seen in the rabbit. In the higher orders (see dog) the copular band is crowded down to the uvular level by the lower end of the paramedian lobe. This is formed by the tonsillar lobule (*ton*) which acquires through the medullary stratum secondary connection with the pyramis. In the Primate cerebellum this downward crowding brings the tonsillar lobule in lateral relation to the uvula. The loop formed by the paraflocculus is in some forms the most conspicuous part of the lobe projecting laterally as the socalled "petrosal lobule" as in the rabbit, woodchuck and monkeys.

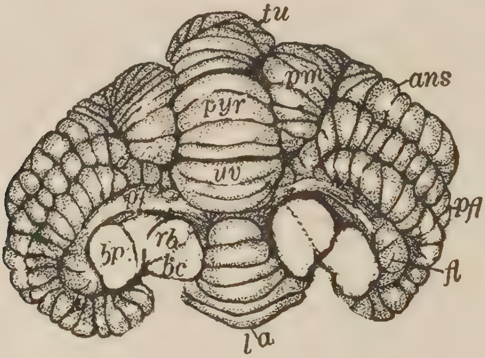

FIG. 66. Cerebellum of a dog, ventral view, × 2.

The paraflocculus is well developed in the quadrupeds and monkeys but in the anthropoid apes (excepting the gibbon) and man it becomes reduced to insignificance though the flocculus is preserved.

The **middle lobe** is bounded in front by the fissura prima (*fp*), posteriorly by the uvular sulcus or fissura secunda (*fs*) and laterally by the parafloccular fissures. It consists of the pyramis (*pyr*) and tuber (*tu*) which are strictly vermian or median lobules. On each side it includes the paramedian (*pm*) and ansiform (*ans*) and lunate (*lun*) lobules united by the concrescence of the lunate lobules in the posterior wall of the fissura prima and over the dorsal border of the cerebellum.

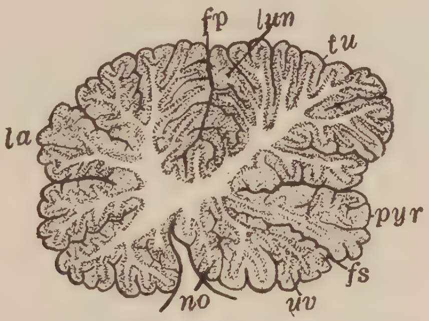

FIG. 67. Cerebellum of a dog, median section, × 2.

The **lunate** or clival **lobules** (*lun*) constitute the front of the middle lobe forming the posterior wall of the fissura prima. They are not only bilateral but unite over the mid-line forming a considerable median lobule or clivus. This is large in the Ungulates (fig. 18). They are separated from the ansiform or semilunar lobule on each side of the **postlunate** or postclival fissure (*pl*). In the lower mammals these lobules are small though the median expanse of the posterior wall of the fissura prima is quite extensive. In the Primates the lateral parts are greatly enlarged forming the (posterior) lunate lobules of human anatomy. A median section will clearly reveal the close relation of the lunate lobules to the remainder of the middle lobe.

The **ansiform lobules** (*ans*) or semilunar lobules of the Primates form on each side a large loop of laterally projecting folia. In the lower orders the lobules are small, limited in front by the postlunate (*pl*) and behind by the postansiform fissures. In the Primates the lobules become greatly elongated due to the great increase in the number and length of the folia. In the lower orders it appears as a single lobule with two limbs; in the Primates these become folded upon themselves in a transverse manner forming thus a superior and inferior semilunar lobule (*ans*). When the great horizontal fissure which separates them is opened it will be seen that the folia run diagonally across its bottom and it may be regarded as a fissure formed by the overgrowth of the two limbs of the ansiform (semilunar) lobe. The superior semilunar lobules are connected across the mid-line by the folium vermis quite intimately combined with the clivus and, like it, relatively undeveloped in the Primates.

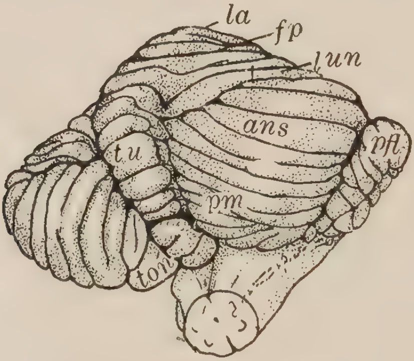

Fig. 68. Cerebellum of a cebus, posterolateral view, × 1½.
For meaning of letters see page xxi.

The **paramedian lobule** (*pm*) on each side is separated in the lower mammals (rabbit, woodchuck, etc.) by a distinct bare medullary area from the median lobule or **tuber vermis** (*tu*). This region is converted into a deep paramedian fissure in the higher mammals as these lobules become crowded together by further growth. Secondary continuities may appear to exist between them, but in reality the tuber and the paramedian lobules are distinct. On the lateral side the deep parafloccular fissure separates each paramedian lobule from the floccular lobe. The straight ladder-like position of the paramedian lobules (*pm*) on the back side of the cerebellum in the lower mammals is well seen in the brain of the woodchuck (fig. 62). Its upper end projects over the ansiform lobule (*ans*) from which it is separated by the postansiform sulcus. Its lower end is crowded down so that in the Primates it comes to be opposite the uvula. Though narrow in the lower orders it becomes greatly expanded in the anthropoids and man. Three subsidiary lobules are recognized (fig. 71). The part which adjoins the ansiform or semilunar lobules is called the gracile lobule (*grc*), secondarily folded in man so that an intergracile sulcus passes across its surface. The lowest part is the tonsillar lobule (*ton*) which comes to lie opposite the uvula in man, and forms an obtrusive feature of the cerebellum. The intermediate part is the biventral lobule (*biv*). These lobules are distinguishable in the lower orders but their homologies to the structures in man can be best demonstrated in the Cebidae (fig. 68).

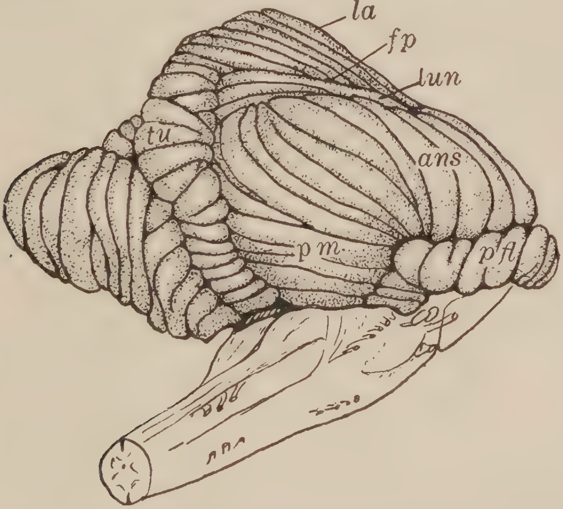

Fig. 69. Cerebellum of a baboon, posterolateral view, × 1½.

The tuber vermis (*tu*) is a narrow median lobule. In the lower orders and in the Primates it is quite straight, but in many of the Carnivora (fig. 63) and Ungulates it becomes twisted to the side in an *S*-shaped manner as a result of its much greater length. Below, it is separated from the pyramis (*pyr*) by the suprapyramidal fissure; above, it joins the folium vermis. It is at its upper end that continuities with the lateral lobules may occur.

The pyramis (*pyr*) is a small triangular median lobule between the tuber and uvula, from both of which it is separated by deep fissures. Its tapering lateral extensions make it easily recognizable on the surface. These in the lower orders and in the course of fetal development join the dorsal limb of the paraflocculus but in the course of further evolution this continuity is lost and secondary continuities with parts of the paramedian lobule may take place.

The medullary center of the cerebellum

Any section through the cerebellum will reveal the central tree-like arrangement of the medullary substance. This consists of nerve fibers that pass to and from the cortex. The whiteness is imparted to it by the myelin sheaths of the fibers. In a median section (fig. 67) a large stem is seen to enter the anterior lobe and give off separate branches into the lobules. The largest stem forms the center of the middle lobe and gives off branches to the several median lobules. Separate small stems are seen in the pyramis, uvula and nodulus. A section to one side through the paramedian lobe will show a similar tree-like arrangement of the medullary center entering the tonsillar, biventral, gracile and ansiform lobules.

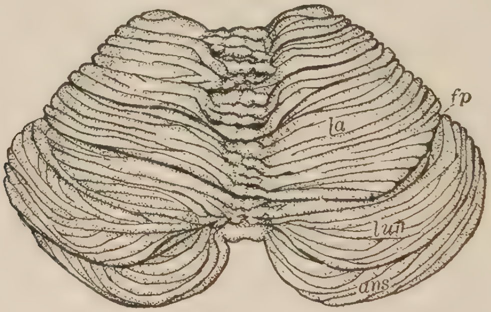

FIG. 70. Cerebellum of a newborn babe, anterior view, × 1½.

To display the lateral extent and lobular disposition of the medullary substance, two other methods may be resorted to: (1) Remove the pia and separate the lobules by opening the fissures to their full depth. Then allow the cortex to dry till it is a light brown, and replace into fluid. The shrinkage of the cortex will be marked, the lobules will be reduced in size and closely shrunken to their medullary center, the disposition of which now can be studied to advantage. (2) With a knife, orange stick or some small suitable instrument remove the cortex and folia of the various lobes, taking first the anterior lobe, then the floccular lobe, then the paramedian and ansiform lobes and lastly the tuber vermis. If this is done systematically with frequent removal of débris (washing off with a stream of water) the arrangement of the medullary center in each lobule can be roughly demonstrated.

The medullary center of the nodulus is a short bow-like structure, that of the uvula is narrow and prolonged backwards; and like those of the pyramis and tuber they are limited to the mid-line or vermis. The great transverse sheet that enters the anterior lobe gives off subsidiary sheets into the smaller lobules. The sheet that enters the semilunar lobule and the ansiform is also an extensive one. On each side of the vermian center are the paramedian centers. The medullary center of the paraflocculus curves forward over the lateral surface of the cerebellar peduncles. If it is stripped away in a backward direction it will be seen to enter the posterior surface near the mid-line.

Further dissection is needed to show the entrance of the three cerebellar brachia or peduncles into the medullary center on each side (fig. 72). If the middle peduncle or **brachium pontis** *(bp)* is traced dorsally it will be seen to spread out into the medullary center of the ansiform and paramedian lobules. The inferior peduncle or **restiform body** *(rb)* enters deeply medial to the brachium pontis and enters into the central or vermian part of the medullary center and that of the anterior lobe. Separate connections appear to enter the floccular lobe through the peduncle of the flocculus and the medullary band that goes to the limits of the paraflocculus. The anterior peduncles or **brachia conjunctiva** *(bc)* appears in front under the medullary center of the anterior lobe. They issue from the deep medial part of the medullary center. In reality each brachium arises from the large cell masses, the dentate and umboliform nuclei, enclosed in each side of the medullary center. They pass forward to enter the midbrain ventral to the inferior colliculi where they cross each other (conjunction) and pass forward to end in the red nucleus and subthalamic region. The uncinate bundle *(uf)* arises in the fastigial nucleus, crosses the mid-line and curving over the

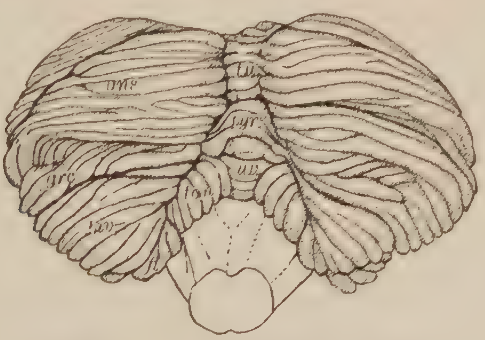

FIG. 71. Cerebellum of a newborn babe, posterior view, × 1½.

upper and outer surface of the brachium conjunctivum enters the vestibular area medial to the other peduncles.

The brachia conjunctiva (*bc*) are united by the **anterior medullary velum.** Under the tonsillar, uvular and nodular lobules separating them from the dorsal surface of the oblongata will be seen the **posterior medullary velum** (*pv*). It is a thin membrane attached to the cerebellum along the peduncle of the flocculus and to the oblongata along its dorsolateral border. It forms the roof of the fourth ventricle and has on its ventricular surface a choroid plexus which extends laterally through the lateral recesses of the ventricle.

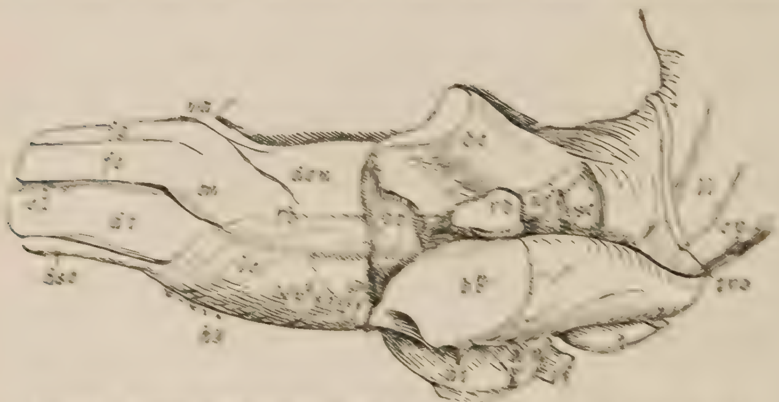

Fig. 72. Cerebellar brachia of a dog. × 1½. For lettering see page xx.

The cerebellum deals exclusively with the motor functions, including posture and movement. Judging from the works of Luciani and others, its cortex may be thought of as a dynamic motor field designed to maintain or alter the rate of flow of excitor impulses into the muscles. It not only reinforces reflex tonus (inherent in the muscular arcs) but also subconsciously maintains all manner of postures (postural tonus) imposed upon the muscles and provides for the precise regulation of the duration, strength and speed of muscular movement. The various areas or lobes of the cerebellar cortex stand in categorical relations with the various functional muscle groups and flexion areas of the body, by means of afferent and efferent fiber systems. Its efferent connections are mediated in part by the vestibular centers and tracts and in part by the red nuclei and rubro-spinal tracts. Its afferent connections are with the muscle spindles, tendon and joint receptors by means of the nerves and tracts that conduct these deep sensibilities.

This proprioceptive function of the cerebellum is a subconscious one, for the cerebellum has in rare cases been entirely wanting without impairment of any of the usual conscious sensibilities. In such cases its motor functions are compensated by the cerebrum.

In the mammals the cerebrum acquires a progressively increasing control over the cerebellar function through the development of the cerebro-ponto-cerebellar connections and the lateral lobes of the cerebellum; so that the dynamic functions of the cerebellum come to be controlled and trained under the selective action of the cerebral cortex.

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CHAPTER 11

THE BRAIN-STEM OF MAMMALS

The cranial nerves and ventral side of the brain-stem

By the term brain-stem we mean that part of the brain which remains after the removal of the cerebral hemispheres and the cerebellum. It is a compact tubular structure with thick walls enclosing a central canal that is converted into ventricles. The cranial nerves are connected with the brain-stem and in its thick walls reflex connections exist for the performance of the special functions of these nerves. The primitive brains of Ichthyopsida (fishes) are little more than such cranial reflex organs although they have already become invaded by (olfactory) connections from the forebrain and (tonic) connections from the cerebellum. In Sauropsida (reptiles and birds), the cerebellar and striatal interconnections are added as a definitive part to the brain-stem and rudimentary conduction systems come into existence. In mammals the motor functions of the highly developed cerebrum, cerebellum and corpus striatum are mediated by a complex system of interconnections that extend throughout the ventral part (peduncular region) of the brain-stem. In addition the brain-stem of mammals is pervaded by great fiber systems for the conduction of cutaneous, muscle-joint and other sensibilities to the cerebellum and cerebrum, and for auditory and visual impulses to the cerebrum.

Thus we find the mammalian brain-stem to be a compact, though highly organized structure with a number of characteristic irregularities in its external contour. It is composed of (1) reflex arrangements in connection with cranial nerves, (2) conduction systems for afferent impulses to cerebellum and cerebrum, (3) efferent cerebellar, striatal and cerebral systems through which these organs exercise their control over the lower motor reflex systems and (4) several other minor nerve mechanisms such as deal with the conduction of taste, heat regulation, tone of blood vessels, and metabolism. Parts of many of these systems are disclosed on the surface but none can be followed out fully in a superficial examination. Thus, fragments of diverse systems are seen which hint at the complex organization of this, the oldest and most fundamental part of the brain.

If any heterogeneous collection of mammalian brains is examined, one will be impressed by the uniform appearance of the brain-stems. But it will be seen that several factors influence the size and proportions of its component parts. In animals such as the mole that have degenerate visual and auditory organs the visual and auditory centers appear reduced. In animals such as many of the lemurs which have large eyes the visual centers appear enlarged. With the increase in size and complexity of the cerebral and cerebellar cortices in the larger and in the higher mammals, especially apes and man, the afferent conduction systems, the thalamus and the efferent cerebral and cerebellar systems are greatly increased in size. When these variations are kept in mind the study of a single well-organized brain-stem such as that of the cat or dog, will exemplify the entire mammalian class (figs. 72 to 79). For explanation of letters on figures see page xxi.

Examine, now, the ventral surface of the brain-stem of a rabbit (fig. 9), a cat (fig. 73) or a dog (fig. 74) and compare it with that of man. The upper level is marked by the **crossing** (chiasma) of the **optic tracts** (*ot*). The lower level is at the attachment of the **first pair** of **cervical nerves** (*c*1). Below this the brain-stem has been cut away from the cervical cord. Crossing over the middle of this surface is the great **pontal protuberance** (*pp*) which forms on each side a **brachium pontis** that leads into the medullary center of the cerebellum. Behind the protuberance is a narrower crossing band, the **lateral lemniscus** (*tb*) or trapezoid body. Together these two structures delimit a segment of the brain-stem called the **pons.** The segment caudal to the pons is the **medulla oblongata** or bulb which extends from the lateral lemniscus (*tb*) to the level of the roots of the first pair of cervical nerves. In front of the protuberance are seen on each side the cerebral peduncles (*cp*) leading upwards and disappearing beneath the optic tracts to enter the **internal capsule** (*int*). The peduncles form the ventral aspect of the midbrain and thalamus, two segments that appear very prominent on the dorsal surface of the stem. The four rounded hillocks or **colliculi** (*sc*, *ic*) characterize the midbrain, concealed entirely on the ventral side by the peduncles (figs. 75 to 79). In front of the midbrain is the thalamus characterized by the geniculate bodies (*mg*, *lg*), pulvinar (*pul*) lateral nucleus (*lat*) and habenular bodies (*hb*). If the optic tracts (*ot*) are followed across the peduncles (*cp*) they are seen to enter the **lateral geniculate bodies** (*lg*) at the posterior border of the thalamus. Thus the thalamus is in large part in front of the optic tracts, although a small ventral portion of it, the **tuber cinereum** (*tc*) and the **mammillary bodies** (*mb*) are seen protruding between the peduncles (*cp*) on the ventral side just behind the optic crossing (*ot*). The small stem leading from the tuber cinereum is the **infundibulum.** Usually it is broken away leaving a torn crevice in the tuber. Its lower end joins the **hypophysis** or **pituitary gland** (fig. 77, *pit*) which also is torn away in the ordinary specimen. Between the peduncles (*cp*) is a space, the **interpeduncular fossa** behind the mammillary bodies (*mb*).

The **cranial nerves and their superficial origins** should now be examined. Be careful in removing the pia not to tear away with it the cranial nerves nor to injure the parts of the brain. The point on the surface of the brain where each cranial nerve appears or attaches is known as the superficial attachment of the nerve. It should be born in mind that the motor nerves arise from large clusters of cells within the brain-stem, known as **motor nuclei** and that the sensory nerves arise from cells in the **sensory cranial ganglia.** There are twelve pairs of cranial nerve bundles although actually there are more cranial nerves since two or more nerve components may be included in one bundle.

1. The **olfactory nerves** (fig. 181, *oln*) consist of nonmyelinated fibers and are invariably torn out of the olfactory bulb (*ob*, 12) when the brain is removed. Each nerve cluster passes through the cribriform plate of the ethmoid in 20 to 30 small filaments, each surrounded by a dural sheath. They at once terminate in the olfactory bulb. The olfactory nerves are sensory and conduct into the bulbs impulses of smell from their cells of origin in the olfactory epithelium. The accessory olfactory or **vomero-nasal nerve** (*aon*) innervates the rudimentary vomero-nasal organ. It is quite small but in an especially prepared specimen (fig. 180) may be seen passing over the medial side of the bulb to enter its dorsal and posterior border.

2. The **optic nerves** (*ot*) consist of nerve fibers that arise from the inner layer of large retinal cells. As they leave the eyeball through the cribriform area of the sclera they become myelinated and form

the large optic nerve. A dural sheath surrounds the nerve. As the nerves enter the cranial cavity a part of their fibers cross to the opposite side. This crossing is the **optic chiasma.** It separates the diagonal band *(db)* from the tuber cinereum *(tc)*. The chiasma is formed by a crossing of the optic fibers from the medial or nasal half of each retina. The fibers from the temporal half remain on

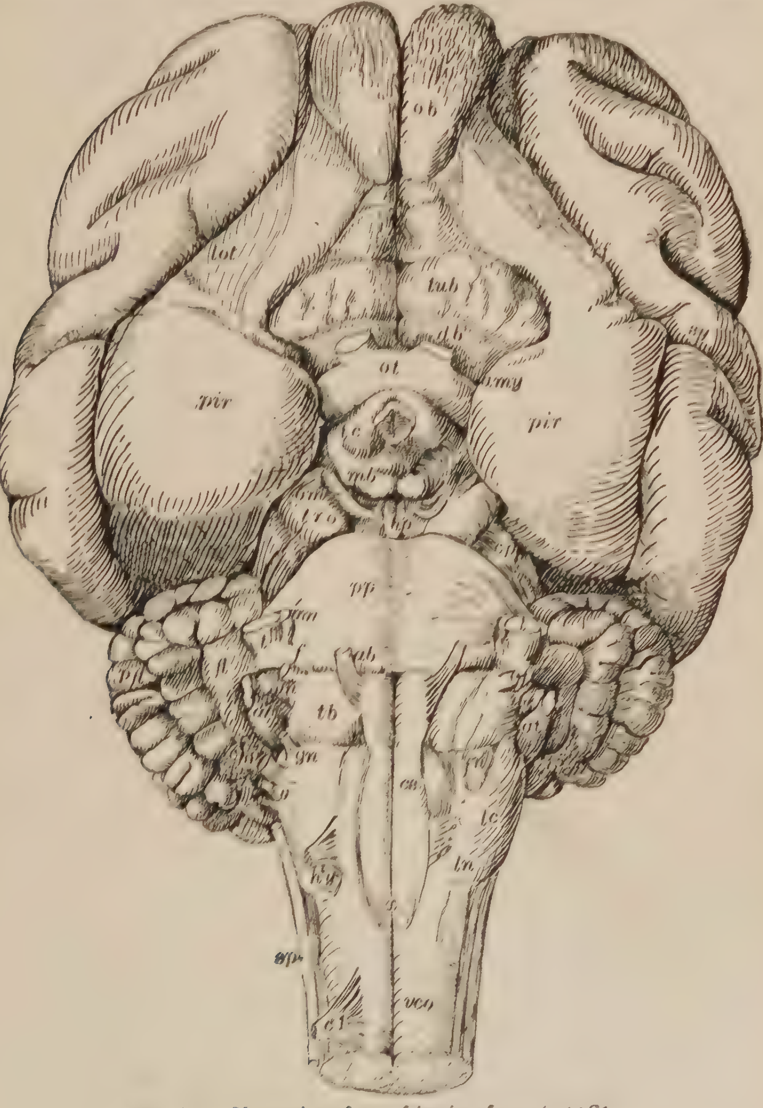

FIG. 73. Ventral surface of brain of a cat, × 2½.

the same side. The chiasma is continued as the optic tracts which embrace the cerebral peduncles (fig. 74). The optic tracts terminate in the lateral geniculate body (*lg*), pulvinar (*pul*) and the superior colliculus (*sc*) of the midbrain as can be seen on the dissected brain-stem. Into these they convey the impulses of vision from the retinae. These fibers are in reality tracts throughout and not true nerves as their name implies, for the retina is derived from the brain during development.

3. The **oculomotor nerves** (*om*) can be identified (figs. 9, 73, 74) as they come out of the interpeduncular fossa over the medial margin of the cerebral peduncles (*cp*). This is their superficial origin. Note their relations to the mammillary bodies (*mb*), optic tracts and hypophysis cerebri. These nerves are motor and supply the medial, superior, inferior recti muscles, the levator palpebrae superioris muscle, the inferior oblique, the ciliary muscle and the constrictor of the pupil. Their origin is from a large nucleus of cells in the midbrain ventral to the cerebral aqueduct (fig. 165, *om*).

4. The **trochlear nerve** (*tro*) of each side will be found as a small filament among the vessels between the brachium pontis and the temporal lobe (figs. 72, 78). It should be looked for between the posterior cerebral and the superior cerebellar arteries. Its superficial origin is from the dorsal side of the midbrain just caudal to the inferior colliculus (*ic*). See special demonstration. The nerve comes from the opposite side and crosses through the anterior medullary velum decussating with its fellow of the opposite side. The nerve arises from a small group of motor cells, the **trochlear nucleus** in the midbrain ventral to the cerebral aqueduct (fig. 163, *tro*). The nerve passes through the tentorial margin, roof of the cavernous sinus, superior orbital fissure to supply the superior oblique muscle in the orbit.

5. The **root of the trigeminus nerve** (*t*) and the small **masticator** nerve (*mn*) take their origin from the postero-lateral side of the brachium pontis. They are also spoken of as **major portion** and **minor portion** of the trigeminus or as **sensory fifth** and **motor fifth.** The **trigeminus** proper or major position is a large sensory (afferent) root bundle that arises in the **trigeminal ganglion** in the lateral part of the cavernous sinus. It passes dorsad beneath the tentorium and penetrates the back part of the brachium pontis. It terminates chiefly as (*dt*) a long descending root (figs. 55, 72, 78, 79) in the pons, oblongata and cephalic part of the cervical cord in

close relation to a special nuclear mass, the **nucleus of the trigeminal nerve** (*tn*). This can be seen on the lateral surface of the oblongata (*bulb*). The nerve is wholly sensory. Its three peripheral branches in the face are the ophthalmic, maxillary and mandibular nerves. They supply the skin of the face, the mucous membrane of the mouth and nose, the teeth, orbital structures and the dura.

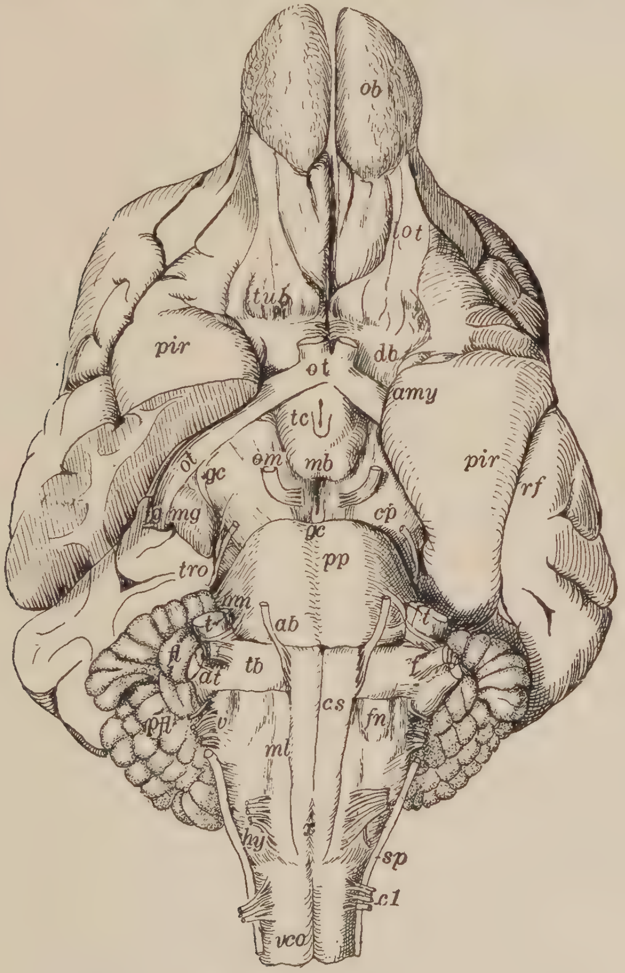

FIG. 74. Ventral surface of brain of a dog, × $1\frac{1}{8}$.

The **masticator nerve** (*mn*) or minor portion will be found leaving the brachium pontis as one or two small strands just ventral to the entering root of the trigeminus. It passes on the ventral surface of the trigeminal ganglion and joins the mandibular division to be distributed to the temporalis, masseter, pterygoids, mylohyoid, anterior digastric, tensor tympani, tensor palatini and levator palatini muscles. It takes origin from an oval nuclear mass in the lateral part of the pons, the **masticator nucleus** or principal motor nucleus of the trigeminus (fig. 151, *mn*). The mesencephalic root and nucleus of this nerve are probably sensory although its peripheral distribution is uncertain.

6. The **abducens nerves** (*ab*) take their superficial origin from the ventral surface of the oblongata (*bulb*) along the posterior border of the pons (between the olive and pyramids (*cs*) in Primates). Be careful not to pull out the nerves. They arise from clusters of cells, the **abducens nuclei** in the floor of the 4th ventricle at the level of the inferior part of the pons (fig. 146, *an*). They pass ventral to the pons, through the cavernous sinuses and superior orbital fissures to the lateral rectus muscles of the eyeball and the retractor bulbi in the lower mammals. They are exclusively motor nerves.

7 (*a*). The **facial nerve** (*f*) will be found closely associated with the cochlear, vestibular and intermedius nerves. It lies on their ventral side. Its superficial origin is on the lateral side of the oblongata (*bulb*) just posterior to the brachium pontis. This triangular space is known as the ponto-cerebellar angle. Dorsal to the facial nerve are the vestibular nerve (*vn*), acoustic tubercle (*at*) and flocculus (*fl*). The facial (*f*) is a motor nerve that takes origin in the oblongata (*bulb*) from a large group of motor cells, the **facial nucleus** (fig. 142). The nerve describes a dorsal loop in the oblongata before leaving its lateral surface. Its peripheral course is through the internal acoustic meatus, facial canal, root of the neck and parotid gland to its distribution in the facial muscles of expression, posterior digastric, stylohyoid and stapedius muscles (fig. 145).

7 (*b*). The **intermedius** or **glossopalatine nerve** (*i*) is closely associated with the facial. It appears as a fine strand between the facial (*f*) and vestibular (*vn*). Its superficial origin is the same as that of the facial. It is a mixed nerve, its fibers being partly afferent and partly efferent. The **afferent fibers** take origin in the geniculate ganglion; their peripheral branches pass in the chorda tympani to supply the taste buds on the anterior part of the tongue; their central branches join the solitary tract (*sf*) in the oblongata (*bulb*). The **efferent** fibers arise in the oblongata from a small

group of cells in the reticular formation in line with dorsal nucleus of the vagus, called the nucleus salivatorius (*mv*). Through the chorda tympani these fibers supply the submaxillary gland and ganglion which in turn supplies the sublingual gland. Through the great petrosal nerve these fibers supply the sphenopalatine ganglion which in turn supplies the mucous membrane of the nose and the palate, and the lacrimal gland. These efferent fibers are chiefly secretory and vasodilator.

8 (*a*). The **vestibular nerve** (*vn*) joins the oblongata (*bulb*) in the angle between the restiform body and the brachium pontis just dorsal to the exit of the facial and intermedius nerves. It is so closely bound to the cochlear that they usually constitute one trunk known as the acoustic nerve. The vestibular is a sensory nerve. It arises from the vestibular ganglion in the bottom of the internal acoustic meatus. The peripheral fibers supply the maculae in the saccule, utricle and ampullae of the semicircular canals. The central fibers constitute the nerve and terminate in the vestibular nuclei in the floor of the fourth ventricle (fig. 128).

8 (*b*). The **cochlear nerve** (*co*) closely associated with the vestibular arises from the cochlear ganglion (fig. 157). The peripheral fibers supply the hair cells of the organ of Corti. The central or root fibers constitute the nerve and enter the acoustic tubercle or cochlear nuclei (*at*). Identify these tubercles (*at*) as compressed gray elevations on the lateral surface of the restiform body (*rb*).

9. The **glossopharyngeal nerve** (*gn*) should be found as a small filament cephalad to the vagus (*v*). It is usually not possible to distinguish its root from that of the vagus except by its more cephalic position. It consists of afferent and efferent fibers. The **afferent fibers** arise from the superior and petrosal ganglia (fig. 133) on the trunk of the nerve. The **efferent fibers** arise from the **ambiguus nucleus** (*am*) and **dorsal efferent nucleus** (*mv*) in the oblongata (*bulb*). Its peripheral distribution is to the tympanum, pharynx and taste buds in the posterior part of the tongue.

10. The **vagus nerve** (*v*) is attached by a series of root filaments to the side of the oblongata in the sulcus between the descending root of the trigeminus (*dt*) and restiform body (*rb*). It consists of afferent and efferent fibers. The **afferent fibers** arise from the **jugular** and **nodosal ganglia** (fig. 133) and enter the vagal nuclei (*va*) or ala cinerea as the solitary fasciculus (*sf*). The **efferent fibers** arise from the ambiguus nucleus and dorsal efferent nucleus

of the vagus in the oblongata (*bulb*). The distribution of the vagus is visceral to the pharynx, larynx, heart, esophagus, bronchi, lungs, stomach, duodenum, liver, intestines and kidneys.

11. The **spinal accessory nerve** (*sp*) will be found to arise superficially by a series of delicate filaments caudal to the root filaments of the vagus from the lateral surface of the oblongata and from the lateral surface of the cephalic portion of the cervical cord. It is a motor nerve that arises from cells in the lateral part of the ventral gray column (figs. 126, 127). The accessory or bulbar portion arises with the vagus (fig. 133) from the ambiguus nucleus in the oblongata and is distributed to the pharyngeal muscles. The **spinal portion** arises from the lateral portion of the ventral gray column of the spinal cord in the upper four cervical segments and is distributed to the sternomastoid and trapezius muscles.

12. The **hypoglossal nerve** (*hy*) will be found to arise from the surface by several root filaments from the ventral side of the caudal portion of the oblongata (*bulb*), lateral to the cerebrospinal tracts (*cs*). It is a motor nerve that arises from the **hypoglossal nucleus** in the floor of the fourth ventricle (fig. 131). Its peripheral course is through the hypoglossal canal and neck, to supply the muscles of the tongue.

Special preparations are necessary to demonstrate the peripheral course of the cranial nerves.

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CHAPTER 12

THE MEDULLA OBLONGATA (BULB)

THE medulla oblongata or bulb is the caudal segment of the brainstem. From the very beginning of vertebrate history it has stood in connection with the gill arches, pharynx and internal organs in their performance of the vital functions of respiration and ingestion of food and regulation of visceral activities. In origin it is a structure even more ancient than the spinal cord or the more anterior parts of the brain, both of which appear to be added by further growth and differentiation. Even the brain of the amphioxus is roughly comparable with the oblongata of true vertebrates.

In the Ichthyopsida (fig. 275) the oblongata is connected by means of the trigeminal and vagal groups of nerves with a highly specialized mandible, gill arch mechanism, pharynx and visceral organs, so that the mechanisms for respiration and ingestion of food are intimately combined. Moreover, the central connections of the trigeminal, vestibular and lateral line nerves and the cerebellum are developed in the pontal region and through the oblongata they acquire connections with the spinal cord.

In the Sauropsida and Mammals the lateral line nerves are suppressed, the gill arches become transformed into other structures of the neck; but the original constitution and functions of the oblongata and pons are retained. Some modifications take place for adapting these functions to air breathing and a terrestrial mode of life. Most noteworthy is the increase in cerebellar connections and the establishment of definitive conduction systems to the cerebellum and to the cerebrum.

Examine the oblongata (figs. 72–79). First identify the cranial nerves. The hypoglossus (*hy*), spinal-accessory (*sp*), vagus (*v*) and glossopharyngeus (*gn*) are connected with the lower oblongata. At its upper end where the oblongata merges with the pons are the facial (*f*), intermedius (*i*), cochlear (*at*), vestibular (*vn*) and abducens (*ab*) nerve roots. Excepting the cochlear and vestibular the nerve roots are rather delicate and are liable to be torn out with the pia.

If they are to be saved a **very careful dissection** with sharp scissors should be done so as to cut the pia away from the nerve roots before it is pulled off. However, specimens that have been stripped off the pia and nerve roots are excellent for the study that follows.

The lower end of the oblongata is at the level of the upper root filaments of the first cervical nerves (*c*1), where it is continued into the spinal cord. This is on the level with the foramen magnum of the occipital bone. The upper level is indicated by the lower border (*tb*) of the lateral lemniscus (trapezoid body) and in Primates by the lower border of the greatly enlarged pontal protuberance (*pp*). Here the oblongata is continued into the pons. It is evident that both levels are arbitrary. The spinal end resembles the cord. The pontal end is greatly modified by the special acoustic and vestibular structures and resembles the pons. A **ventral median fissure separates** the two halves. The conspicuous white band along each side of this fissure is the **cerebrospinal** or **pyramidal tract** (*cs*). These tracts disappear in the fissure at the lower level of the oblongata (*x*) where each intercrosses with its fellow of the other side. Just below the lateral lemniscus (*tb*) and lateral to the cerebrospinal tracts (*cs*) a small eminence produced by the facial nucleus (*fn*) is often seen in the lower mammals. In Primates there appears in this region a large oval eminence produced by the inferior olive. In some of the lower orders a slight olivary eminence is seen just lateral to the lower extent of the cerebrospinal tract. The eminence seen in a more lateral position is the **nucleus lateralis.** From this a large sheet of laterocerebellar or **external arcuate fibers** (*lc*) is seen passing dorsally into the restiform body (*rb*). They cover the descending root of the trigeminal nerve (*dt*) and the restiform body (*rb*). Just behind the external arcuate fibers (*lc*) is an elongated tubercle with depressed margins formed by the **descending root of the trigeminal nerve** and its nucleus (*dt*). Ventral to this the surface of the lower end of the oblongata is formed by the **ventral and lateral white columns** (*vco*) of the cord continued upwards to the nucleus lateralis and beyond lateral to the cerebrospinal tracts to disappear beneath the lateral lemniscus (*tb*) and pontal protuberance (*pp*).

On the dorsal surface (figs. 78, 79) the dorsal white columns of the cord are seen to pass up into the oblongata and enlarge into three columns on each side which separate to form the obex. The fasciculus gracilis (*fg*) is the slender one on each side of the mid-line.

In many animals it is so small and depressed that it scarcely appears on the surface. At the obex it enlarges over the nucleus gracilis (*ng*) or clava which separates from its fellow like the forks of a *Y* to form the lateral boundaries of the obex. The fasciculus cuneatus (*fc*) is the large ascending bundle lateral to the gracilis. It also enlarges as it covers the cuneate nucleus (*cn*) below the obex and as it turns laterally on a level with the obex. Here it turns up under cover of the external arcuate fibers (*lc*) and covers an irregular nuclear mass, the **nucleus of the restiform body** (*rb*) or lateral cuneate nucleus. The descending root of the **trigeminal nerve** (*dt*) overlying its own nucleus is seen as a distinct wide ridge with depressed margins just lateral to the fasciculus and nucleus cuneatus.

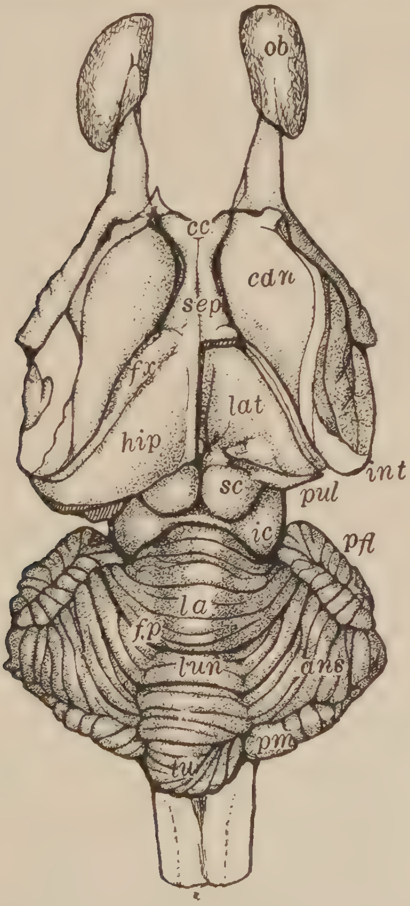

FIG. 75. Brain stem of a dog (with cerebellum), dorsal view, × 1¼.

Above, it disappears from view under the external arcuate fibers (*lc*). The dorsal spinocerebellar tract (*dsc*) unites with these fibers to join those from the nucleus of the restiform body to pass forward as a rounded column, the restiform body (*rb*). This (*rb*) forms the lateral border of the oblongata and turns dorsally to enter the medullary substance of the cerebellum (fig. 72). The restiform body is formed by afferent fibers which connect the oblongata and the spinal cord with the cerebellum. In the human brain another system of arcuate fibers, the reticulo-cerebellar fibers (*rc*) appear on the ventral surface and join the restiform body. Arcuate nuclei may appear in them. This long arcuate system is related to the pons. Note how the cochlear nucleus (*at*) is hung over the restiform body where this turns up into the cerebellum (figs. 78, 79). In Primates the acoustic stria (*as*) can be seen leaving the cochlear nucleus, crossing the restiform body and floor of the fourth ventricle to disappear along the mid-line. In the lower mammals it is beneath the surface.

The posterior medullary vellum (fig. 77, *pv*) is attached to the dorsal medial side of the restiform body (*rb*) and crosses laterally behind the cochlear nucleus to form the pouch of the lateral recess (*lr*) through which the choroid plexus (fig. 73, *chp*) is seen protruding. For the floor of the fourth ventricle see figure 128.

The pons

The pontal protuberance (*pp*) is the prominent external feature of the pons. Three structures enter into its formation. The large cerebral peduncles (*cp*) enter it from above; the cerebro-pontal tracts end there, while the cerebrospinal tracts (*cs*) pass through to descend in the cord. The large nuclei of the pons (*np*) surround the entering cerebro-pontal tracts (*cpo*) which end in them. The fibers that form the brachia pontis (*bp*) arise from these pontal nuclei, intercross in the mid-line and on each side extend as the brachia into the medullary center of the cerebellum. The roots of the trigeminal nerve (*t*) and the masticator nerve (*mn*) pass through or are caudal to the brachium pontis.

Behind the pontal brachia, crossing the surface on each side, is a wide band, the trapezoid body (*tb*) or crossing of the auditory or lateral lemniscus (*ll*). Note its origin from the acoustic tubercle (*at*) that juts out just below the flocculus (*fl*). The large cochlear nerve that comes from the cochlea has been torn out of this nucleus (*at*) giving it a ragged appearance. The lateral lemniscus (*tb*) disappears beneath the cerebrospinal tract (*cs*) so that its further course through the pons is not visible. It intercrosses with its fellow of the other side and then turns upwards medial to the brachium pontis, and reappears above it on the lateral surface of the other side (figs. 72, 79) turning dorsally to enter the **inferior colliculus** (*ic*) in front of the cerebellum. In the Primate brain the crossing (*tb*) of this band of auditory fibers is not seen on the ventral surface for it is entirely covered over by the backward growth of the pontal protuberance (*pp*).

Under the cochlear nucleus (*at*) and quite fused with it, is the root of the vestibular nerve (*vn*) which cuts right through the origin of the lateral lemniscus (*tb*) from the cochlear nucleus (*at*). Ventral to the vestibular nerve the root of the facial (*f*) passes through the upper border of the lateral lemniscus. Beneath this may be seen the ridge formed by the descending root of the trigeminal nerve (*dt*).

On the dorsal surface are seen the brachia conjunctiva (*bc*) connected across the mid-line by the anterior medullary velum (*av*). The entrance of the several brachia into the medullary center can now be followed out as described on page 103.

The fourth ventricle

The fourth ventricle (fig. 77, *fv*) is the large rhomboidal space formed by the expansion of the central canal between the oblongata and pons ventrally and the cerebellum and medullary vela dorsally. It can best be examined when the cerebellar brachia have been cut away (fig. 128). The caudal half over the oblongata is wide and triangular with prominent lateral extensions or recesses over the cochlear nuclei (*at*). Here its lateral boundaries are formed by the diverging gracile nuclei (*ng*) and the restiform bodies (*rb*). These furnish a delicate line of attachment (tinea) for the posterior medullary velum. This velum forms the posterior roof of the fourth ventricle. It is compressed by the nodulus (*no*) and uvula (*uv*) of the cerebellum. It is a thin membrane attached to the cerebellum along the peduncle of the flocculus. It has on its ventricular surface a pair of choroid plexuses which extend laterally over the restiform bodies through the lateral recesses (*lr*) of the ventricles. These plexuses are seen protruding through the lateral apertures over the cochlear nuclei (*at*) and ventral to the flocculus (*fl*). At the obex a median aperture exists. Through the median and lateral apertures the cerebrospinal fluid which is secreted by the choroid plexuses into the ventricles is allowed to escape into the subarachnoid spaces on the external surface of the brain. Over the surface

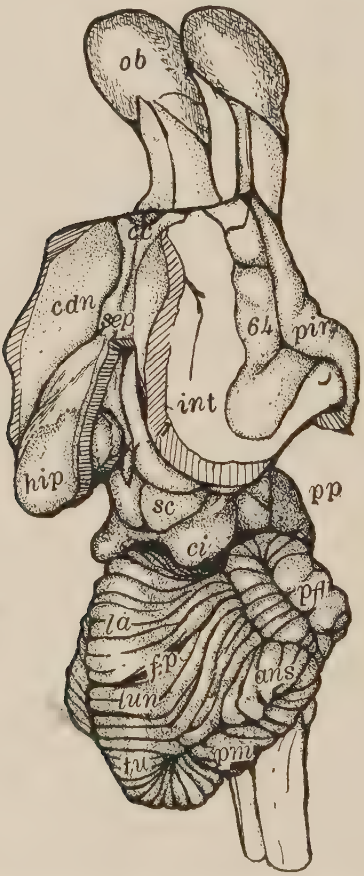

Fig. 76. Brain stem of a dog (with cerebellum), dorsolateral view, × 1¼.

of the brain it flows upward and through the arachnoid granulations enters the blood in the superior sagittal sinus.

The upper half of the ventricle extends over the pons; it is much narrower than the lower half. The brachia conjunctiva (*bc*) form its lateral boundaries. They are united by the anterior velum (*av*) which forms its roof. The lingula and alar lobule of the cerebellum rest on this.

The **floor of the fourth ventricle or rhomboid fossa** should now be examined (figs. 78, 128). It is important to appreciate at the outset that this is the inner or central surface of the oblongata (*bulb*) and pons whose lateral walls have been splayed out, associated with a great spreading of the posterior medullary velum and overgrowth of the cerebellum. The floor is divisible into the lower and upper portions that belong to the oblongata and pons respectively. A line through the region of the cochlear nuclei (*at*) separates the two portions. Thus the lateral recesses and a part of the vestibular area (*dvn*) are included in the lower portion. The lateral boundaries of this are the rèstiform bodies (*rb*) and gracile nuclei (*ng*). The caudal limit is marked by the obex and here the ventricle receives the opening of the central canal beneath the ala cinerea or vagal nuclei (*va*). The upper or pontal portion is limited laterally by the brachia pontis (*bp*) and brachia conjunctiva (*bc*). Its cephalic limit is at the caudal level of the inferior colliculi (*ic*) in the cerebral aqueduct. A **median sulcus** separates the floor into two symmetrical halves.

The **lower oblongatal portion** should now be examined. Care should be taken **not to touch it with your instruments and to prevent drying and shrinkage.** A hand lens of low magnification is very useful for making observations on small brains. The fresher the specimen the more favorable it is for study. The **obex** is a thin portion of pia that joins the two eminences of the gracile nuclei (*ng*). Just ventral to the obex note the **nuclei of the vagi** or of the **alae cinereae** (*va*). Note how these join at the obex but above are continued lateral on each side as a wing of gray matter, the **ala cinerea** or **nucleus of the vagus nerve** (*va*). Since the lower union is a part of these nuclei where they unite to descend for a short distance beneath the gracile nuclei it is also spoken of as the **commissural nucleus of the vagi.** The gracile nuclei may be fused cephalad to the obex so as to hide completely the commissural nucleus. Between the alae cinereae (*va*) make out the eminence just lateral to the mid-line formed by the cephalic end of the **nucleus of the hypoglossus nerve.** Further cephalad this eminence is continued as a flattened area, the nucleus intercalatus. Note a furrow, the **sulcus limitans,** lateral to the intercalate and hypoglossal eminence. The large area lateral to this sulcus that extends along the medial surface of the restiform body and brachium pontis is the **vestibular area** formed by the large **vestibular nuclei** (*dvn*) and descending vestibular root (*dvr*). The medial portion of this area (*dvn*) that extends down and disappears between the gracile and cuneate nuclei is the descending vestibular nucleus. The swelling on the medial side of the brachium pontis is due to the medial and lateral vestibular nuclei, and that due to the **superior vestibular nucleus** (*svn*) is medial to the brachium conjunctivum. The **vestibular nerve** (*vn*) penetrates the lateral side of the oblongata ventral to the restiform body to reach the lateral and superior vestibular nuclei.

The **cochlear nerve** terminates in the acoustic tubercle or dorsal and ventral cochlear nuclei (*at*). The **dorsal cochlear nucleus** (*at*) is seen as a finger-like, semilunar elevation of gray matter moulded over the restiform body where this turns dorsad to enter the cerebellum. In the human oblongata the **medullary** or acoustic striae (*as*) pass from the medial end of the dorsal cochlear nucleus towards the mid-line where they disappear from view. Interposed in the stria near the mid-line there can often be seen one or more gray nodules, the nuclei fasciculi teretes which should not be confused with the nucleus intercalatus in cross sections. The acoustic striae (*as*) consist of fibers that pass from the cochlear nucleus (*at*) to the opposite side of the pons and constitute the dorsal part of the *decussation* (crossing) of the **lateral** or **auditory lemniscus** (*ll*).

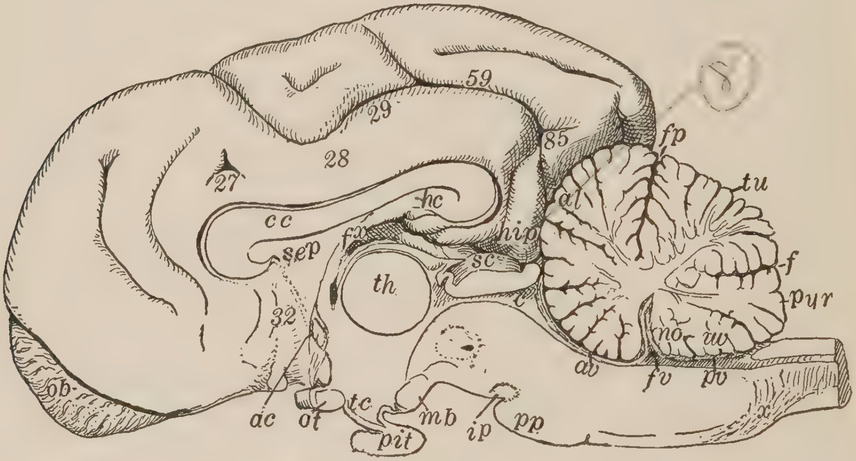

FIG. 77. Medial view of oblongata and pons of a dog, × $1\frac{1}{6}$.

The intermedius, glossopharyngeal (*gn*) and vagus (*v*) nerves penetrate the lateral wall of the oblongata (arcuate fibers (*lc*) and descending root of the trigeminus) to reach the ala cinerea (*va*). The hypoglossal nerve (*hy*) arising from its nucleus beneath the ala penetrates the oblongata to its exit on the ventral side.

Remove the anterior medullary velum and examine the pontal portion of the floor of the fourth ventricle. On each side of the median sulcus a white band, the **medial longitudinal fasciculus** (*mlf*), may often be seen. More laterally it is covered over by a flat mass of gray matter, the nucleus incertus (*inc*). Near the middle may be seen another elevation caused by the internal bend or genu of the facial nerve (*f*) and by nucleus of the abducens nerve. The sulcus limitans separates the eminence of the nucleus incertus and facial genu from the superior vestibular nucleus (*svn*) and a band of fibers that leads forward from this (*vm*). These overlie the masticator nucleus and the main trigeminal nucleus.

Along this line you may see in the human brain a rusty streak, the **locus caeruleus** caused by a pigmented nucleus of the same name. Its connections are not known. It must not be confused with the **nucleus of the mesencephalic root of the trigeminus** which has a more cephalic position but is not pigmented and cannot be seen on the ventricular surface.

Now determine how the **facial, abducens** and **masticator nerves** must pass through the pons and oblongata to reach the points of their exit. How must the trigeminal nerve pass to reach its nucleus?

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CHAPTER 13

THE MIDBRAIN, THALAMUS AND STRIATE BODY

REMOVE the pia from the midbrain (figs. 75 to 79). Be careful not to pull off with it the trochlear nerves (*tro*) which cross through the anterior velum and also the pineal body which is attached to the dorsal side of the thalamus.

The midbrain extends from the pons to the thalamus. On account of the oblique position of the brachia pontis (*bp*), the upper part of the pontal protuberance (*pp*) projects beneath the midbrain. The four rounded elevations called hillocks or **colliculi** or quadrigeminal bodies form a very distinctive feature on the dorsal side of the midbrain. For meaning of letters on figures see page xxi.

The **inferior colliculi** (*ic*) are solid projecting rounded nuclear masses united by a bar-like commissure (*cic*) which gives them a dumb-bell appearance. The posterior concavity of this is occupied by the anterior lobe (*la*) of the cerebellum. A large columnar band of fibers, the auditory or lateral lemniscus (*ll*) appears under cover of the anterior margin of each brachium pontis and turns dorsally to enter the inferior colliculus. This fiber tract comes from the cochlear nuclei of the opposite side. Its crossing (*tb*) is seen on the ventral surface behind the pontal protuberance (*pp*). A larger band of fibers, the brachium colliculi (*bic*) connects the inferior colliculus with the medial geniculate body (*mg*) on each side of the brainstem. This body is a large nuclear mass of the thalamus that has been protruded caudally over the lateral surface of the brachium colliculi which thus ends in its medial surface. Their junction is crossed on the surface by the small transverse peduncular tract (*tp*). The lateral side of the medial geniculate body is crossed by the large optic tract (*ot*). Ventrally it rests on the cerebral peduncle (*cp*), but here a small band of fibers may be seen in some brains (fig. 74) passing into the optic tract. This is the geniculate commissure (*gc*) which in reality loops around the ventral side of the brain-stem with the optic tracts to enter the medial geniculate body of the other side. Under cover of the optic tracts (not seen on the surface) a large band of fibers, the auditory radiations (fig. 160, *ar*), leave the anterior side of the medial geniculate body to turn laterally into the internal capsule and end in the transverse temporal gyrus (68) in Primates, or the postsylvian gyrus (68) in lower orders.

The auditory radiations form the final link in the auditory conduction system that extends from the cochlea to the temporal cortex. It is formed by a linking together of the cochlear nerve, the lateral lemniscus, the brachium colliculi and the auditory radiations. The cochlear ganglion, cochlear nuclei, inferior colliculi and medial geniculate bodies are cell masses from which each one of these fiber systems take origin. This is a conduction system added to the brain-stem in the Sauropsida and Mammals.

Look now for some minor details. On the lateral surface of the midbrain (fig. 79) a small triangular tegmental area (*bi*) is seen bounded ventrally by the cerebral peduncle, in front by the collicular brachium and behind by the lateral lemniscus. In this area just ventral to the origin of the brachium is a small elevation, the bigeminal nucleus (*bi*). Ventrally it gives off a flat tract of fibers (*bip*) that curve in front of the lateral lemniscus to disappear under the anterior margin of the pontal protuberance (*pp*). This band conceals a slight elevation caused by a nucleus.

On their posterior surface the inferior colliculi lie against the anterior lobe of the cerebellum. Here (fig. 78) they are united by the anterior medullary velum (*av*) which further back also unites the brachia conjunctiva (*bc*). These are seen to disappear beneath the colliculi, medial to the lateral lemnisci. Here the trochlear nerves (*tro*) are seen to intercross through the anterior medullary velum (*av*). In the human brain the velum behind the colliculi is quite thick, with a median ridge, the frenulum of the velum.

The **superior colliculi** (*sc*) are rounded eminences or gray caps that form the roof or tectum over the anterior part of the midbrain. They are closer together than the inferior colliculi and, like them, are united by a commissure that has, however, a greater median extent (fig. 77). Posteriorly they lie against the inferior colliculi. Their lateral margins are embraced by the collicular brachium (*bic*). Their anterior margins receive a large tract of optic fibers (*ot*) that bends over the posterior surface of the thalamus. This broad band is seen in front of the colliculi which it appears to unite with the thalamus. Note that it is in this region that the transverse peduncular tract (fig. 79, *tp*) ends.

The superior colliculi are chiefly optic reflex centers in which the functions of convergence, divergence and conjugate binocular movements, as well as accommodation and pupilo-constriction are mediated. In addition to this through the tectospinal and tecto-olivary tracts they control the movements of the head. They receive the large spinotectal tracts which probably bring in to them cutaneous sensibility.

The cerebral peduncles and interpeduncular region

The cerebral peduncles (*cp*) are large descending fiber tracts that cover the ventral surface of the midbrain and thalamus on each side (figs. 73 and 74). They appear under cover of the optic tracts where they come out of the internal capsule and lower down they disappear by entering the pontal protuberance. They are formed by important systems of fibers that connect the forebrain with all of the other parts of the central nervous system. Their dorsal surfaces make functional connections with the midbrain and subthalamus. They consist of four fiber systems. These cannot be seen on the surface as separate bands.

(1) The cerebro-spinal and cerebro-bulbar tracts arise in the motor area of the cerebral cortex and pass down through the internal capsule (*int*) to enter the middle part of the cerebral peduncles. The cerebro-bulbar tracts end on motor nuclei in the pons and oblongata. The cerebro-spinal tracts pass through the pontal protuberance, appear again on the ventral surface of the oblongata (*cs*) and disappear at its lower level where they cross (*x*) to the opposite side to descend in the lateral column of the cord and end on the motor nuclei of the cord. These are the tracts through which voluntary movements are performed.

(2) The fronto-pontal tracts arise from the frontal cortex in front of the motor area. They pass down through the internal capsule in the medial fifth of the peduncles and end in the protuberance in the pontal nuclei. Their functions are not known. But it is known that tumors in the premotor area produce a peculiar lack of motor inhibition known as perseveration or persistence of movement or posture. (A. S. K. Wilson.) It may be that through these tracts the cerebrum is able to inhibit cerebellar activity.

(3) The parieto-pontal tracts arise in the parietal cortex, possibly in the post-central area (area of muscle and joint sensibility). Their precise region of origin is not known; even an occipital and temporal origin is assigned to them. They are large tracts that pass down in the internal capsule and lateral two-fifths of the peduncles to end in the pontal nuclei. Their functions are not known, but it is known that stimulation of the post-central area in the apes facilitates the performance of the responses of the motor area mediated by the cerebro-bulbar and -spinal tracts. It may be that through these tracts the cerebrum is able to facilitate or excite cerebellar activity. (Graham Brown.)

(4) The ansa lenticularis, the strio-bulbar and strio-subthalamic tracts are added to the peduncles at the level of the optic tracts and tuber cinereum. They may be seen on the medial side of the peduncles bordering the tuber, but for the most part they are on the dorsal surface of the peduncles hidden from view. Behind the optic tracts three bulgings may be seen in the peduncles caused by the substantia nigra, subthalamic nucleus and nuclei reticulares subthalami. The view that the corpus striatum through the ansa lenticularis and the nuclei reticulares subthalami exercises a steadying or inhibitory influence over the dynamic cerebellar functions has been put forth by A. S. K. Wilson.

Between the diverging cerebral peduncles is seen the large gray tuber cinereum (*tc*). Anteriorly it is bordered by the optic tracts and their crossing (*ot*). Caudally it terminates in the two white rounded mammillary bodies (*mb*). These are quite separate in the higher mammals but become more closely united in the brains of lower forms. By means of a hollow stalk, the infundibulum, the tuber is connected with the hypophysis cerebri (*pit*), a glandular organ (fig. 77). In the ordinary specimen, the hypophysis and the infundibulum are usually pulled away from the tuber leaving a torn crevice in its ventral surface.

Below the mammillary bodies is the interpeduncular fossa bounded on either side by the cerebral peduncles. Here the roots of the oculomotor nerves (*om*) come out penetrating in part through the medial border of the peduncles. In the Rodents, Ungulates and other lower orders a small gray mass, the interpeduncular nucleus, is seen in the bottom of the fossa just in front of the pontal protuberance. In higher forms it is concealed by the overgrowth of the protuberance. In many specimens (fig. 73) one can see a pair of white bundles, the habenulo-peduncular tracts (*hp*) which end in the nucleus and cover its surface with a white stratum. On each side, lateral to the nucleus and tracts, another white band can sometimes be seen, the mammillary peduncle (*mp*) which passes up through the root of the oculomotor nerve and enters the lateral side of the mammillary body by turning sharply ventrally. The name, posterior perforated area, is applied to the bottom of the interpeduncular fossa on account of the number of fine holes from which small blood vessels have been pulled out when the pia was stripped off.

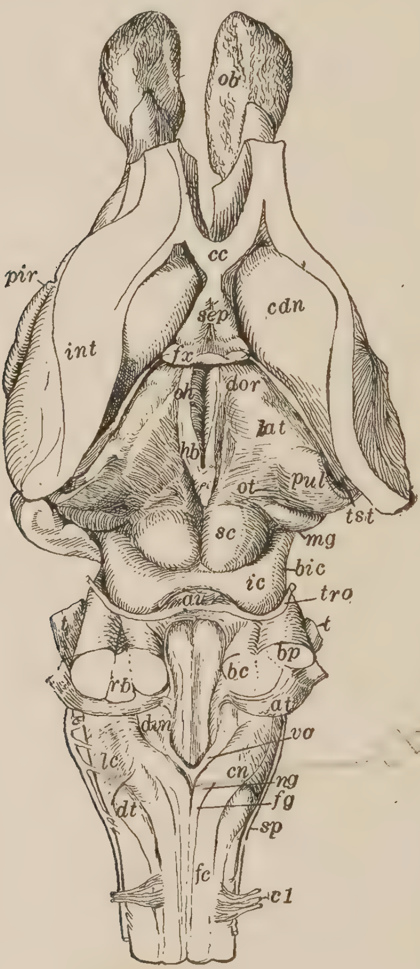

FIG. 78. Brain stem of a dog, dorsal view, × 1½.

The thalamus or diencephalon

The thalamus (*th*) or interbrain is the segment of the brainstem just above the midbrain and medial to the internal capsule. On its dorsal and posterior surface it is surrounded by the hippocampus, fornix and velum interpositum (fig. 55). When these have been removed (fig. 78) the dorsal and posterior surface of the thalamus will be exposed. The third ventricle is a vertical cleft that quite completely separates the thalamus into two halves, hence its name diencephalon. Their dorsal edges are united by a narrow strip of choroid tela which forms the roof of the third ventricle (not seen in the figures). From this a narrow double choroid plexus projects into the third ventricle. Dorsal to the pineal body the tela forms a small recess. When the tela is torn away two inconspicuous lines of attachment or medial tenia thalami appear along the medial margins of the two thalamic halves. Along the lateral surface close to the groove in which passes the terminal stria (*tst*) will be seen the lateral tenia thalami, a line along which the lateral choroid plexus has been torn away.

If the optic tract (*ot*) be traced from the chiasma around the cerebral peduncle (*cp*) it will be found to turn dorsally into the posterior part of the thalamus. Here it passes between the medial geniculate body (*mg*) and the internal capsule. It ends in a small mass, the lateral geniculate body (*lg*) just in front of the medial geniculate (*mg*) and also in the pulvinar (*pul*) a much larger mass which forms the dorsal and most posterior projection of the thalamus. A careful scrutiny will show that a wide band of the optic fibers, the optic stratum (*ot*), passes across the posterior surface of the pulvinar medially and turns backwards to disappear in the front end of the superior colliculus.

It should be appreciated that the lateral geniculate body, pulvinar and superior colliculus are cellular masses in which the optic tracts end. The superior colliculi are centers which mediate the various ocular reflexes, such as convergence, divergence, conjugate movements of the eyes, focusing on near objects and pupillary movements. The pulvinar and lateral geniculate body on the other hand send a large band of the thalamo-cortical fibers, or optic radiations, through the adjacent dorsal part of the internal capsule into the visual area of the occipital cortex.

Note how the medial geniculate body (*mg*) is surrounded by the optic tract, pulvinar and optic stratum in front, and the cerebral peduncle ventrally. It receives the brachium colliculi (*bic*); it is connected with its fellow of the other side by the geniculate commissure (*gc*) and it gives rise to the auditory thalamo-cortical radiations (*ar*) to the postsylvian or transverse temporal gyrus.

In the dog and most other animals the frontal margin of the pulvinar is usually defined by a shallow depression. Under the optic stratum (*ot*) medial to the pulvinar a bulging is seen, produced by the centrum medianum or posterior nucleus of the thalamus. This is a cell mass relatively large in the lower mammals and is designated as the pulvinar by some authors. In front of the pulvinar and the optic stratum another broad bulging is evident, that of the dorsal surface of the large lateral nucleus of the thalamus (*lat*). This great cellular mass receives the medial lemniscus through the brain-stem and sends a great system of thalamo-cortical radiation into the postcruciate and coronal or postcentral regions of the cerebral cortex. These radiations pass through the middle or dorsal part of the internal capsule (*int*) with a forward inclination.

Where the front end of the thalamus narrows behind the downturned columns of the fornix it presents a prominent oval bulging formed by the anterior nucleus of the thalamus (*ant*). It receives a large bundle of fibers, the mammilo-thalamic fasciculus of Vicq d'Azyr, from the mammillary body. It emits a flat band of fibers laterally under the terminal stria that radiate forward into the caudate nucleus.

The white bands seen in the medial margin are the medullary stria of the thalamus or olfactohabenular tracts (*oh*). If the columns of the fornix (*fx*) are drawn forward it will be seen that these tracts unite with the columns where they sink into the medial wall of the thalamus. This union forms the ventral border of the interventricular foramen. Traced back each tract ends in an elongated gray enlargement, the habenular nucleus (*hb*). Note how far forward these nuclei extend. A delicate habenular commissure unites the two nuclei seen extending as a loop towards the pineal body (*pin*). A large compact tract of fibers, the habenulo-peduncular tract or retroflex bundle of Meynert, arises from each habenular nucleus and pierces the medial wall of the midbrain to end in the interpeduncular nucleus (*ip*) on the ventral surface.

The lateral surface of the thalamus cannot be seen in an ordinary dissection for it lies against the internal surface of the cerebral peduncle (internal capsule) to which it contributes streams of thalamocortical fibers. This relation can be seen in a cross section of the brain taken through the middle of the thalamus (fig. 170).

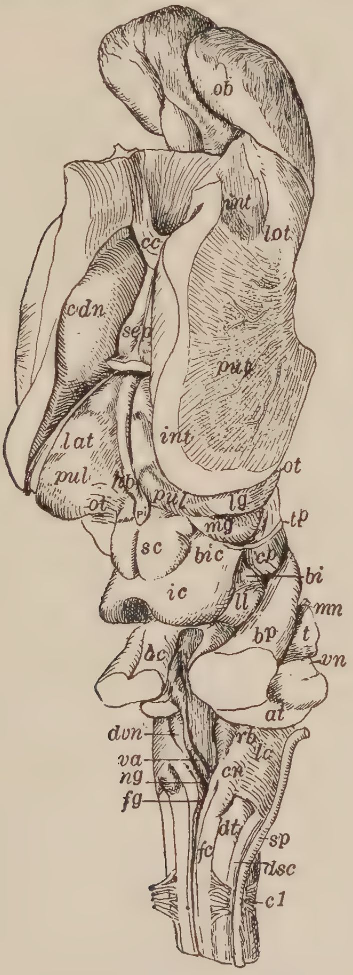

Fig. 79. Brain stem of a dog, dorsolateral view, × 1½.

The **third ventricle** (figs. 77, 78) is the median cleft-like space that separates the two thalamic halves. Notice that the dorsal border of this cleft is formed by the olfactohabenular tracts (*oh*) which end posteriorly in the habenular bodies. The two halves are united by a delicate habenular commissure which unites the posterior parts of the thalamic halves. In the middle the thalamic halves are united by an extensive round adhesion, the soft commissure (*th*) which partly obliterates the third ventricle. To study the medial or ventricular side of the thalamus, secure a brain, split into two halves by a median section, and compare with figures 6, 51 and 77. In such a section (fig. 77) the delicate choroid tela, which forms the narrow roof of the third ventricle and is attached on each side along the medullary stria, is often torn away. The posterior part of the roof is formed by the pineal body. The floor is formed by the optic chiasma (*ot*), tuber cinereum (*tc*), and mammillary bodies (*mb*) united along the mid-line. Its posterior wall is formed by the union of the tegmental regions of the midbrain, but at its dorsal level the ventricle is continued as the cerebral aqueduct (*c*) under the colliculi. The anterior wall is formed by the terminal lamina through which crosses the anterior commissure (*ac*).

In the platypus (fig. 51) and the kangaroo (fig. 52) it will be seen that the part of the terminal lamina dorsal to the anterior commissure is occupied by the dorsal or hippocampal commissure, a primitive condition quite like that seen in Reptilia (fig. 220). The extreme anteromedial position of the hippocampal formation and the absence of a true corpus callosum in these low orders should be noted. This condition is repeated in the fetuses of higher mammals before the corpus callosum makes its appearance. The corpus callosum (*cc*) grows in on the dorsal side of the hippocampal commissure. As it expands (compare rabbit, fig. 6; dog, fig. 77, and any of the Primates) it displaces the hippocampal formation backwards over the side of the thalamus; with it the hippocampal commissure and the columns of the fornices which form its borders are stretched out over the dorsal surface of the thalamus. Thus in the higher mammals the dorsal division of the terminal lamina may be regarded as uniting the two fornices and joining them to the under surfaces of the corpus callosum. As the corpus callosum invades the medial walls of the two hemispheres it becomes flexed down at both ends and buckles dorsally away from the underlying fornices. And thus there is drawn into the interval between them a thin plate of nervous tissue, the septum pellucidum (*sep*), derived from the preterminal area (32) of each medial wall of the hemisphere.

The interventricular foramen (of Monroe) is seen just posterior and above the anterior commissure in front of the thalamus. It unites the lateral ventricles of each side with the third ventricle and the cerebrospinal fluid formed by the choroid plexuses of the lateral ventricles (*chp*) flows backwards into the third and thence by way of the cerebral aqueduct (*c*) into the fourth ventricle to escape into the subarachnoid spaces by way of the lateral and medial apertures over the acoustic tubercle and at the obex.

The striate body

The **striate body** (corpus striatum) forms the basal portion of each hemisphere. It consists of two large cellular masses, the caudate and lentiform nuclei, between which the cerebral peduncles and thalamo-cortical fibers pass as the internal capsule on their way to the cerebrum. Viewed from the ventricular side (figs. 55, 75, 76, 78) the striate body of each side appears to be a forward and lateral continuation of the thalamus. Viewed from the lateral side it appears to be a continuation of the base of the olfactory stalk (fig. 76).

The **caudate nucleus** (*cdn*) is a comma-shaped gray mass whose large head is seen in the lateral ventricle of which it forms the floor and lateral wall. Its narrow tail curves backwards and down into the temporal horn of the ventricle to join the amygdala. It is accompanied by the terminal stria (*tst*) which connects the amygdala forwards with the motor olfactory striatum in the olfactory tubercle (*tub*). In the stria is seen the caudate vein that spreads over the inner surface of the caudate nucleus. The stria and the vein lie in the groove between the thalamus (*lat*) and the caudate nucleus (*cdn*). The subcallosal bundle (*ct*) is a thin band of fibers that occupies the lateral angle between the corpus callosum and the caudate nucleus and is spread over the head of the nucleus. As the callosum is lifted away this sheet of fibers will tend to separate from its under side. The lateral surface of the caudate nucleus is closely applied to the inner surface of the internal capsule. This can be shown by forcibly drawing the internal capsule laterally and thus separating it from the caudate nucleus, or by scraping away the head of the nucleus. At the same time it will be seen that the numerous bands of caudate tissue penetrate into the capsule.

The **lentiform nucleus** (fig. 79, *put*) in its posterior part is situated on the outer surface of the internal capsule opposite the subthalamic region with which it is in intimate connection by fiber tracts that pass through the cerebral peduncles. In front it unites with the head of the caudate nucleus ventral to the anterior border of the internal capsule. This frontal portion forms the motor olfactory striatum within the olfactory tubercle (*tub*). The ventral surface of the lentiform nucleus is covered from before backward by the cortex of the olfactory tubercle (*tub*), pyriform area (*pir*), amygdala (*amy*) and optic tracts (*ot*). Its outer surface is covered by four layers: (1) the cortex of the insula and sylvian and anterior ectosylvian gyri (fig. 76), (2) a layer of white substance, (3) a thin cellular layer called the claustrum (fig. 177) and (4) the external capsule derived in large part from fibers of the anterior commissure (*ac*) which cross through the upper part and are spread over the outer surface of the lentiform nuclei (*put*). These relations can be best seen in a series of cross sections in this region.

Such sections show that the cephalic region of the striatum forms the motor olfactory striatum (*ost*) ventral to the anterior commissure. It is seen that the lower part of the lentiform nucleus consists of a large lateral part, the putamen (*put*), a small fibrous medial part, the globus pallidus (*gp*). It is this part that is connected with the subthalamic region by fiber tracts.

The **amygdala** is a large oval nuclear mass situated within the medial tip of the pyriform area. The cortex of the latter covers it and a functional relation between them is probable. The amygdala is in continuity with the extreme caudal part of the caudate nucleus and lateral olfactory nucleus. It receives the descending or temporal division of the anterior commissure. The terminal stria (*tst*) connects it forward with the striatum in the olfactory tubercle.

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CHAPTER 14

MENINGES, SPINAL NERVES AND SPINAL CORD

THE **vertebral** canal is a flexible tube formed by the vertebrae united in a series by **vertebral ligaments.** It lodges the spinal cord, its meninges and the roots of the spinal nerves.

The **meninges of the spinal cord** are the three membranes which ensheath the cord and are continued through the foramen magnum into those that surround the brain (fig. 80). The **dura mater** is the thick fibrous external membrane whose function is protection and support for the cord, nerve roots, and cerebrospinal fluid. In the **cranial cavity** it also forms the inner periosteal lining of the bones of the base and dome of the skull and carries the special meningeal (dural) vessels. The **arachnoid** is a thin reticulated membrane which carries in its interstices the cerebrospinal fluid which washes and supports the cord and brain. The **pia mater** is the vascular membrane closely encapsulating the cord and brain and carries the numerous spinal and cerebral vessels.

Spinal nerves and roots

The **spinal nerves** are arranged in pairs. They constitute the peripheral nerve trunks that connect the cord with all parts of the body excepting the facial region of the head. The chief areas of distribution are the skin (cutaneous nerves), skeletal muscles (muscular nerves) and viscera (splanchnic, visceral or sympathetic nerves). The spinal nerves pass through the **intervertebral foramina** (*for*) where each nerve forms a short compact trunk (fig. 81). This divides lateral to the foramen into a **dorsal division** (*dd*) to the long muscles and skin of the back, a **ventral division** (*vd*) to the lateral and ventral body wall and the extremities and a **visceral division** (*vis*) (rami communicantes) to the thoracic and abdominal viscera. The dorsal divisions retain a simple segmental arrangement. The ventral divisions form the **cervical** and **brachial plexuses** (fig. 81, *vd*), the **intercostal nerves** and the **lumbar sacral**

plexus. The visceral divisions form the **sympathetic chain** and the various nerves and plexuses distributed to the viscera including all blood vessels and glands of the skin. The cervical nerves and some of the lumbar and sacral nerves have no visceral divisions or white rami communicantes, but they receive fibers from the sympathetic ganglia.

The **roots of the spinal nerves** (fig. 81) connect the nerves with the spinal cord. Each nerve is connected with the cord by a sensory dorsal (*dr*) and ventral motor (*mr*) root. Examine the position and length of the nerve roots. You will note that the cervical nerve roots are short and pass laterally into the intervertebral foramina. The lower cervical and the **thoracic nerve roots** become progressively longer caudally. On account of the gradual shortening of the cord these nerve roots have to pass farther caudally to enter the corresponding foramen, and thus form the cauda equina of the sacral region (fig. 80).

The **dorsal roots** (*dr*) separate into quite a number of root filaments which enter the cord along the dorsal lateral sulcus and form the dorsal root zone of the cord. Traced laterally these roots enter the vertebral foramina where they are seen to emerge from the dorsal **spinal ganglia** (*gang*). Beyond the ganglia the dorsal roots join the ventral roots to form the spinal nerves (figs. 80 and 83). The dorsal roots of the spinal nerve are also spoken of as **afferent, receptive** or **sensory roots** because they consist almost wholly of these nerve fibers that conduct nerve impulses from the receptive endings (receptors) in the skin, muscles, mucous membranes and other receptive areas, into the spinal cord.

The **ventral roots of the spinal nerves** (*mr*) spring from the ventro-lateral surface of the cord by a number of root filaments (fig. 81). These are scattered more transversely along the ventro-lateral surface of the cord. The fibers that compose the ventral roots of the spinal nerves arise from the motor cells of the broad **ventral gray column** (horn) of the cord. The most medial fibers of the root filaments pass into the dorsal divisions (*dd*) of the spinal nerves and supply the long muscles of the back. The musculature of the ventral and lateral body wall and of the extremities is supplied by fibers that have a more lateral exit. The most lateral root filaments in the thoracic region enter the visceral divisions (*vis*, white rami communicantes) of the spinal nerves and from the preganglionic fibers of the visceral motor system. (See chapter 18.)

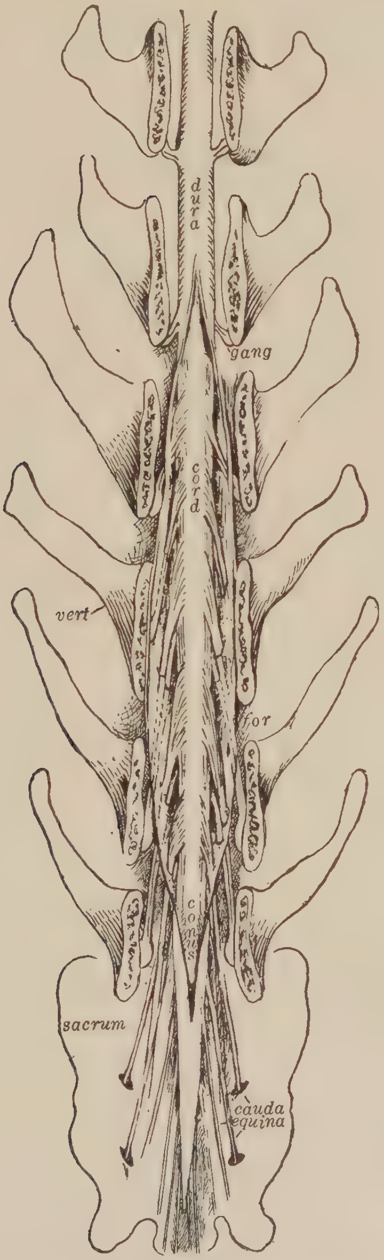

FIG. 80. Dorsal view of spinal cord of a dog at the lower end. The dura has been opened to show cord and dorsal nerve roots.

The **spinal accessory nerve** (fig. 126, *sp*) is the eleventh cranial nerve, but its spinal portion, as the name implies, takes origin from the spinal cord. It arises in the upper cervical region by a longitudinal series of fine root filaments from the lateral surface of the cord about half way between the dorsal and ventral roots of the upper cervical nerves.

The spinal cord

The **spinal cord** (medulla spinalis, figs. 80, 81) is the slender cord-like portion of the central nervous system that occupies the meninges within the vertebral canal. By means of the paired spinal nerves it is connected with all parts of the body below the facial region. Through the fibers of the dorsal nerve roots it receives afferent impulses which it conducts to the motor centers in the cord and to higher correlation centers. Through the fibers of the ventral roots it discharges efferent impulses into the muscles and glands. Moreover, the cord is connected with the brain by a number of ascending and descending tracts which mediate cerebellar and cerebral connections of the highest importance.

The **extent, length and subdivisions of the cord** should be determined on the specimen. The **caudal end of the cord** ends in a conical point, the **medullary cone** (fig. 80, *conus*) the pial sheath of the cord is continued as the **terminal filum** from the tip of the cone to the back of the coccyx. It will be found as a glistening band among the lower lumbar and the sacral nerve roots. The **cephalic end of the cord** is directly continued through the foramen magnum into the **medulla oblongata** (*bulb*) (fig. 73). In fact the caudal unexpanded portion of the oblongata gives the appearance of a somewhat modified cord. The arbitrary plane of division between the two is marked by the upper root filaments of the first cervical nerves (*c*1). Since these are hard to find a more obvious landmark is the level of the foramen magnum. In cross sections the **decussation** or **intercrossing** (*x*) of the **cerebrospinal tracts** in the ventral side is the landmark used. In the ventral surface in this region, the cerebrospinal tracts (*cs*) are seen to cross through the **ventral median sulcus** and therefore obliterate it for some distance. The crossing can best be seen on a specimen from which the pia has been removed.

The average length of the cord varies with the length of the trunk of the animal. Up to the third month of intrauterine life the human cord occupies the entire length of the vertebral canal. Thereafter the spine and canal elongate more rapidly and for a longer time, till at birth the tip of the medullary cone is opposite the 3rd lumbar vertebra. This relative shortening of the cord occurs in most other mammals to a lesser extent. It is of advantage since the chief purpose of the fiber tracts of the cord is to connect the various segments of the cord with each other and upward with the brain.

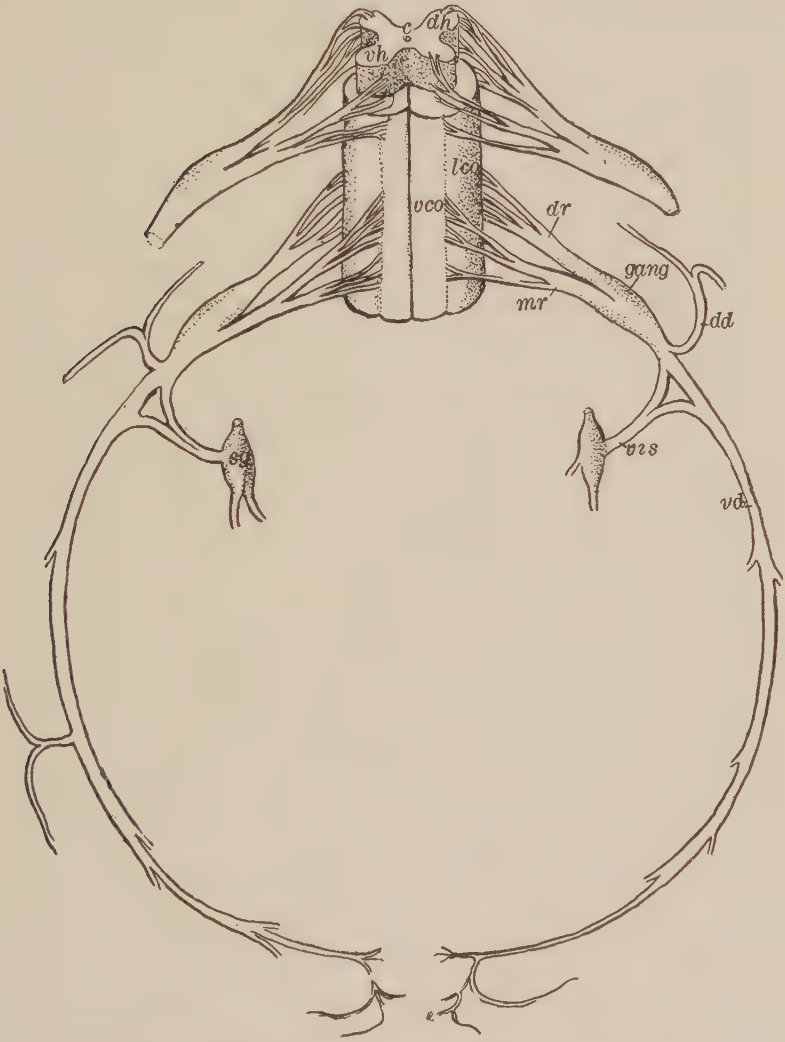

Fig. 81. Schematic view of two spinal cord segments, showing arrangement of white and gray columns, nerve roots and divisions of nerves.

Each portion of the cord connected with a pair of nerve roots is spoken of as a **cord segment** and takes the number and name of the nerves (fig. 81). Thus there are in man one coccygeal, five sacral, five lumbar, twelve thoracic and eight cervical segments; they are arbitrary divisions assigned to each pair of nerve roots. The very primitive (neuromeric) segmentation of the cord is only a transient feature of the developing cord. The primitive segments are soon merged to form a columnar arrangement of both the white fibrous substance and the gray cellular substance of the cord. This is due to the fact that the longitudinal connections between the segments are a dominant feature of the cord, and the cord is never a completely segmented structure. The cord is divisible into **cervical, lumbar, sacral and coccygeal portions.** These portions correspond to the various groups of nerve roots and accordingly vary in length and number of segments in different mammals.

The **external features of the cord** should be examined closely. Beneath the pial sheath the surface of the cord is seen to consist of white substance; this is composed chiefly of nerve fibers, each surrounded by a **sheath of myelin** which imparts to them the white appearance. Nowhere does the cellular substance and neuropile which forms the *H*-shaped core of the cord come to the surface. The cord gradually enlarges from its caudal to its cephalic end. This is due to the gradual accession of nerve fibers in its outer part. In the lumbar and cervical portions the cord is enlarged. The **lumbar enlargement** extends from the medullary cone to the lower thoracic segments and is due to the increase of cellular substance, neuropile (gray matter) and nerve fibers (white matter) connected with the lumbodorsal plexuses that are distributed to the lower limbs. The **cervical enlargement** extends from the middle cervical to the 1st thoracic segments and is due to an increase of cellular substance, neuropile, and nerve fibers connected with the brachial plexuses that are distributed to the upper limbs. The thoracic portion is more slender than the other portions.

The cord is a bilateral structure consisting of two **lateral halves** united by a narrower intermediate portion (fig. 82). The line of separation is marked by a **dorsal septum** and by a median ventral fissure. These should be examined also at the cut end of the cord. The dorsal sulcus is shallow and in its place a median **dorsal septum** extends into the cord between the two halves. Note the depth of the ventral fissure. The narrower mass of substance between the dorsal septum and ventral fissure is the intermediate part of the cord that unites the two halves.

On the dorsal surface of the cord (figs. 78, 79) is seen the **dorsolateral sulcus** along which the dorsal **root filaments** (*dr*) enter the cord. On each side of the dorsal sulcus there is seen a slender column of white substance, the **fasciculus gracilis** (slender bundle), extending the entire length of the cord (*fg*) and gradually increasing cephalad. This consists of the ascending divisions of the dorsal root fibers of the sacral, lumbar and thoracic nerves. In these regions its lateral part forms the root zone. Lateral to it in the upper thoracic and cervical regions there is seen a larger column, **the fasciculus cuneatus** (wedge-shaped bundle) gradually increasing cephalad (*fc*). This consists of the ascending divisions of the dorsal root fibers of the cervical nerves. Its lateral part is formed by the root zone of these nerves. The fasciculus gracilis and cuneatus conduct chiefly muscle and joint sensibilities, cephalad to the oblongata, cerebellum, thalamus and cerebrum. Along the line of the dorsal root filaments another small root bundle, **dorsolateral tract** (of Lissauer) is to be looked for, but it is best seen in stained sections. This tract consists of the fine lateral root fibers which discharge impulses of pain, heat, cold and perhaps tactile sensibility into the cord.

On the **ventral surface of the cord** (fig. 81) on each side of the ventral fissure is seen a large **ventral column** (or funiculus) of white substance (*vco*). It consists of a number of tracts descending from the brain. These are not distinguishable as separate tracts, but on the surface of the cord as well as in sections appear as a single large white column between the ventral roots and the median fissure. Examine the **lateral surface of the cord.** It is formed by the **broad lateral column** (funiculus) of white matter between the ventral and dorsal roots. This consists of several indistinguishable tracts both ascending and descending. Between the issuing ventral root filaments the ventral column is continued into the lateral column (*lco*). The interior of the cord is occupied by an *H*-shaped formation of gray matter (fig. 106). This consists of nerve cells embedded in a fretwork of minute interlacing fibers. Each limb of the *H* represents a longitudinal column of gray matter extending the entire length of the cord. The dorsal portion of each limb is known as the **dorsal gray column** or horn (*dh*) and stands in functional connections with the fibers of the dorsal root (*dr*). Since this column receives the incoming impulses it is also spoken of as the **sensory center of the cord** or **nucleus of termination of the dorsal spinal nerve roots.** Since some of its cells give rise to long ascending tracts that relay some of the impulses to higher centers they constitute also the great relay centers of the cord. The ventral portion of each limb is known as the **ventral gray column** or horn

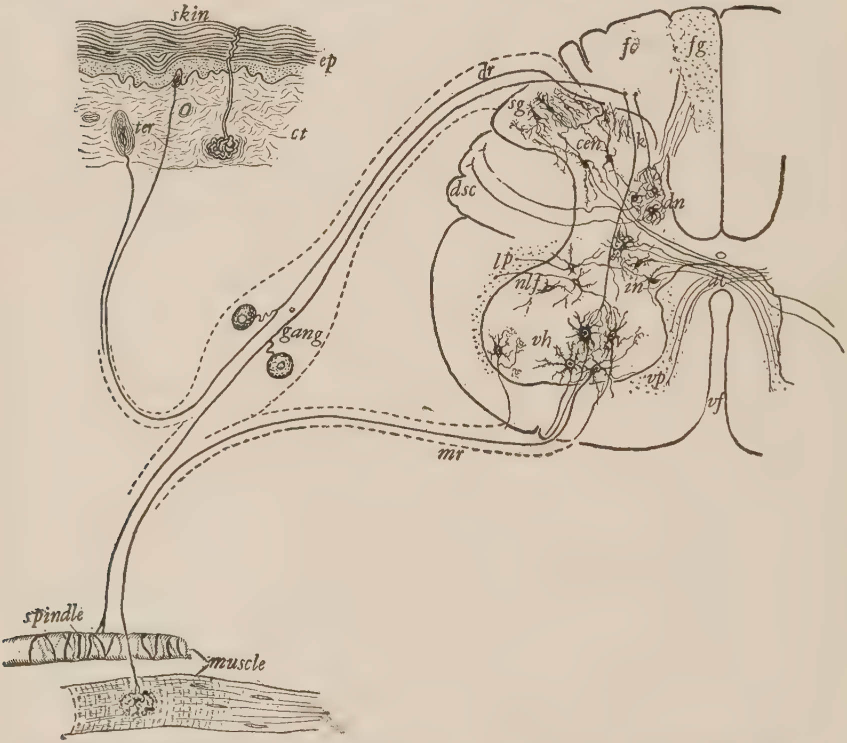

FIG. 82. Diagram of sensory and motor neurones that form a simple reflex arc. For meaning of letters see page xxi.

(*vh*). It is much broader than the dorsal column. Since its cells give rise to the fibers of the ventral roots, it is also spoken of as the **motor column of the cord.** The cross piece of the *H* is the **gray commissure** and represents poorly developed portions of the embryonic neural tube. In the center can be seen the minute **central canal** (*c*). Since it contains a central canal the cord is, strictly speaking, a tube, even in the adult. The outer surface of the gray matter forms the internal contour of the dorsal, lateral and ventral white columns.

REFERENCES

Any textbook or atlas of anatomy.

PART II

MICROSCOPIC STRUCTURE OF THE MAMMALIAN NERVOUS SYSTEM

CHAPTER 15

SENSORY ENDINGS, NERVE TRUNKS, SPINAL GANGLIA

THE **nerves** constitute the fiber systems for conduction of excitation processes commonly called nerve impulses between the peripheral structures of the body and the central nervous system. Sensory and motor fibers, though alike in structure, conduct in the opposite direction and have a different mode of origin as well as different central and peripheral connections. The **sensory fibers** arise from cells in the spinal ganglia or sensory cranial ganglia and are distributed as two branches (fig. 82); one, entering the dorsal root, ends on the dorsal horn of the gray matter (fig. 104), and the other enters the nerve trunk and is distributed in some peripheral areas such as the skin or muscle. The **motor fibers** arise from cells in the ventral horn of the cord and through the ventral root enter the nerve trunk to be distributed to some peripheral structure such as a muscle, gland, vessel or visceral organ.

Cutaneous nerves are so called because they supply the skin. The **skin** besides serving as a protective covering, and secretory surface, serves also the purpose of extensive sense organ. Practically all portions of the skin are reached by the sensory **cutaneous nerves.** Branches of the **trigeminus nerve** supply the skin of the face, mucous membranes of the mouth, nose and the conjunctiva, cornea and eyeball in general (fig. 92). The **cutaneous branches of the cervical plexus** supply the skin of the occipital region, ventral neck region and shoulder girdle. The **posterior divisions of the spinal nerves** supply the skin of the back. The intercostal and upper lumbar nerves supply the skin over the side and ventral surface of the thorax and abdomen. **Cutaneous branches** of the brachial plexus supply the skin of the arm, forearm and hand. The **lateral cutaneous femoral, posterior cutaneous femoral nerves** and **branches of the femoral** and **sciatic nerves** supply the skin of the buttocks, thigh, leg and foot. Branches of the **sacral nerves** supply the skin of the perineum and external genitals. The skin area to which a spinal nerve is distributed is known as a dermatone. Figure 83 shows the dermatones of a monkey.

Sensory nerve endings

Peripheral arborizations or telodendria of the cutaneous nerves are the several minute varicose or skein-like branches into which **each nerve fiber** or axone ultimately divides to terminate in the skin or subcutaneous tissue. Each set of telodendria ends in a special variety of **sensory nerve-endings** or receptors, and is believed to respond only to stimuli of a specific character such as touch, pressure,

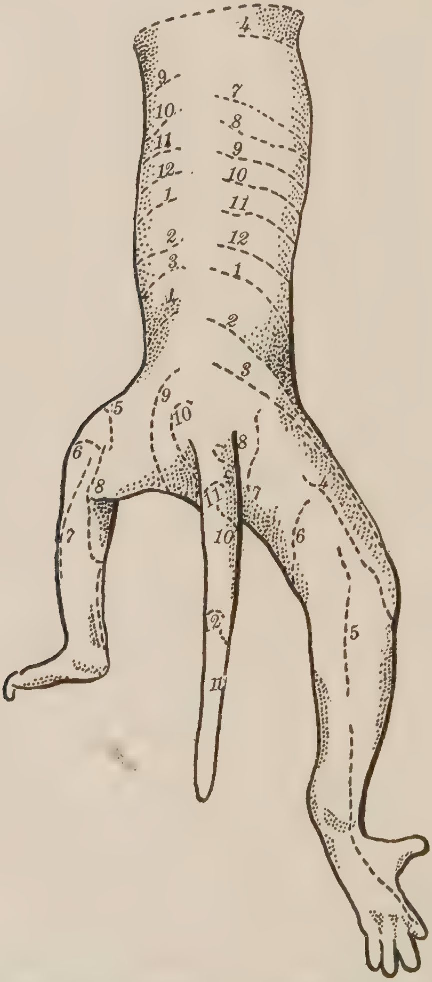

FIG. 83. The skin-fields of the afferent spinal roots of the monkey (macacus rhesus) showing their general arrangement in trunk and hind limb. On the right side the posterior limit of each field is shown, on the left the anterior limit, each designated by the number of the thoracic or lumbo-sacral nerve. After Sherrington.

pain, heat, cold, etc. Each area of skin is supplied by telodendria from several fibers with endings of a specific character; so that each small area of skin has a variable supply of touch, pressure, pain, heat and cold endings. These are not crowded closely but are somewhat separated and are recognized as touch spots, pressure spots, pain spots, warm spots and cold spots. The methods of studying the various kinds of cutaneous sensibility belong to physiology and clinical medicine and will not be discussed here. Anatomically the following endings are described but their relation to the various sensory spots has not been definitely established.

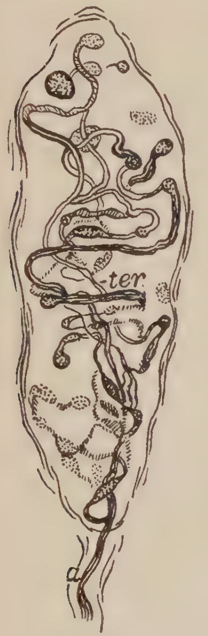

FIG. 84. Nerve ending in Meissner's receptor. After Dogiel.

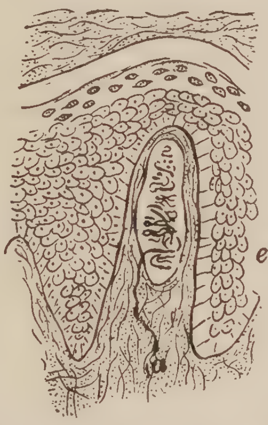

FIG. 85. Meissner's receptor in connective tissue papilla of the skin.

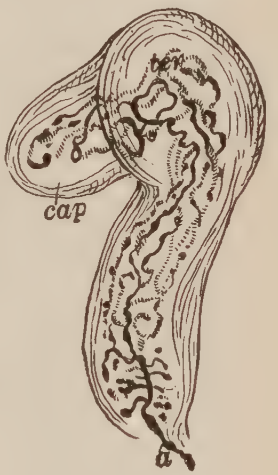

FIG. 86. A modified Pacinian receptor in nail bed. After Dogiel.

Sensory end organs or receptors in the skin should now be studied from the various text books and journals placed in the laboratory. Excepting the receptors of Meissner and the Pacinian receptors, they are difficult to prepare for laboratory study (by the intravitam methylene blue and silver methods developed by Bethe, Cajal, Dogiel, Huber, Retzius and others). Only a brief description follows; for fuller details see text books of histology. All the following figures are greatly enlarged microscopic views of special preparations.

The **receptors of Meissner** can be studied in a section of skin. Each ending consists of a series of flat connective tissue cells surrounded by a thin capsule (fig. 85). At its base it is invaded by a terminal sensory nerve fiber that ends in irregular loops and flattened varicocities between the flat cells (fig. 84). The silver method shows that these nerve terminals consist of a neurofibrillar network.

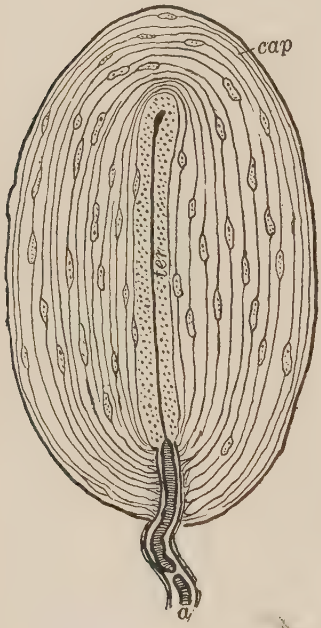

FIG. 87. Pacinian receptor in connective tissue sheath. After Cajal.

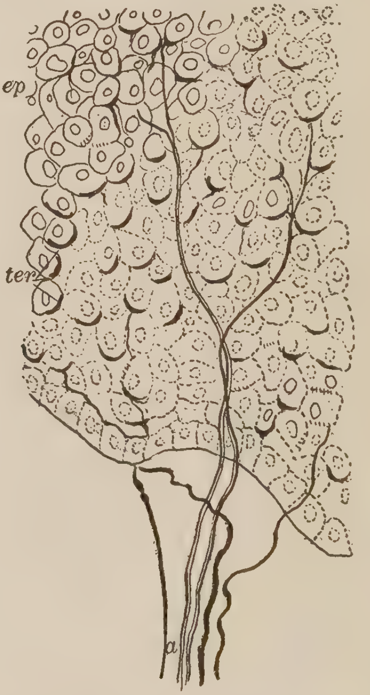

FIG. 88. The disc receptors of Merkel in the epithelium of the nipple of an ape. After Martynoff.

These receptors are supposed to respond to (touch or) tactile stimuli. Their distribution favors this view. They are found in the subepidermal connective tissue papillae of the skin of the palms, soles, nipples, lips, eyelids and other parts of the skin. They are most numerous in the palmar skin of the fingers. The **end-bulbs** of Krause and similar endings (fig. 86) are found in the deeper connective tissue layers of the skin. They vary greatly in size, and are often very large. From two to ten telodendria enter each receptor, depending on the size. The nerve endings are varicose, forming an interlacing skein.

The **genital receptors** and probably also end-bulbs of Krause are regarded as responding to contact stimuli. Encapsulated genital receptors that occur in the glans penis are shown in figures 89 and 91.

The **Pacinian receptors** are large oval structures consisting of a large number of concentric layers of connective tissue enclosing in the center a simple or considerably convoluted or branched nerve ending (fig. 87). These receptors are distributed in the deeper parts of the dermis of the hands, feet, over the joints, tendon sheaths, intermuscular septa, periosteum of the bones, in the epineural sheaths of some nerve trunks (fig. 100), near large blood vessels, in the peritoneum, pleurae, pericardium and mesentery.

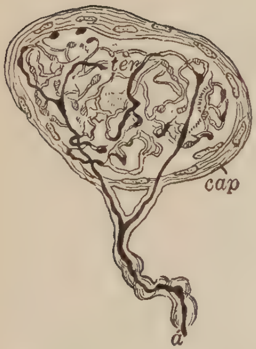

FIG. 89. A genital receptor in the glans penis of man. After Dogiel.

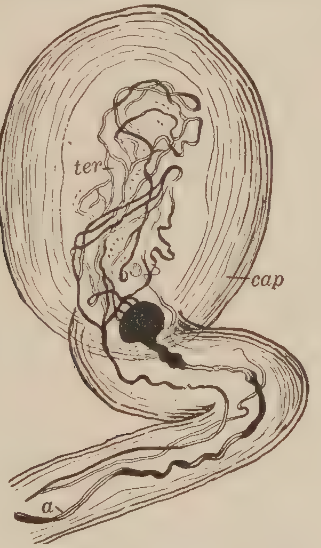

FIG. 90. A Golgi-Mazzoni receptor in the teat of a cow. After Martynoff.

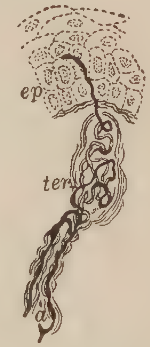

FIG. 91. A genital receptor in the penis of a rat. After Dogiel.

The **cylindrical end-bulbs of Krause** (fig. 86) resemble a Pacinian receptor in structure, excepting that they are much longer, often coiled, and the connective tissue lamellae are fewer. They may be regarded as a transitional form between the Pacinian and Meissner receptors. The nerve ending is not very complex, terminating in a small enlargement, and is as a whole embedded in a semifluid core. These endings are found in the deeper parts of the dermis, in the mucous membrane of the mouth and in the tendons. Pacinian receptors and the cylindric end-bulbs of Krause are supposed to respond to contact or pressure stimuli. The Golgi-Mazzoni receptors (fig. 90) are similar endings with a more complex nerve terminal. They also occur in regions subjected to pressure.

Nerve endings in hair follicles (fig. 93) are especially well developed where the hairs are exposed to contact, as the long whiskers on the lips of Carnivora. The nerve endings form a ring about the neck of the hair follicle. The straight and forked endings run parallel to the base of the hair. External to the latter are the circular plexiform endings; and in relation to the surrounding epithelium note the disc-like endings resembling the tactile discs of Merkel. These endings are regarded as responding to tactile stimuli that move the hair.

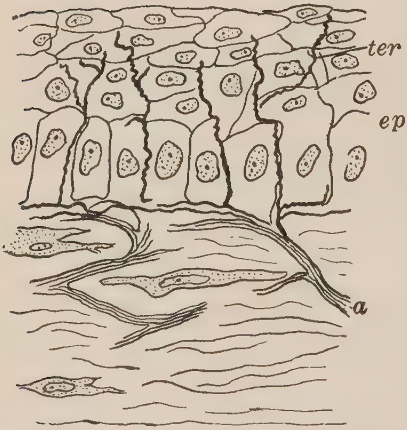

FIG. 92. Free nerve terminals in the epithelium of the cornea. After Cajal.

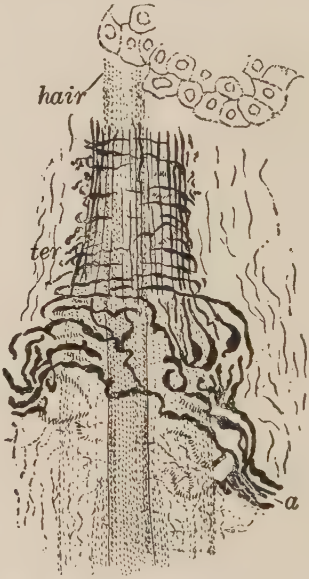

FIG. 93. Nerve endings about a large hair of a dog. After Bonnet.

The **disc receptors of Merkel** (fig. 88) are found in the epithelial layers of the skin and mucous membranes. Their name "tactile discs" implies that they respond to irritative tactile stimuli, as in the case of other endings, for example, the corneal (fig. 92). They are in reality free endings that stand in close relation to the chemical environment of epithelial cells. The nerve fiber divides beneath the epithelium. The branches penetrate the epithelium and end in numerous discs in relation to the surface of the cells. They are found in the skin of the breast (nipple), gums and elsewhere.

Free varicose endings (figs. 94–95) not included in the foregoing varieties are found in abundance in the epithelial and connective tissues of the skin and mucous membranes, and in the deep fascias and ligaments. Since they occur in the ear drum, gums, teeth and cornea (fig. 92), that is, in places which give sharp painful responses, it has been suggested that these endings may serve as pain receptors. Whether any of the foregoing endings respond to heat and cold is not definitely known.

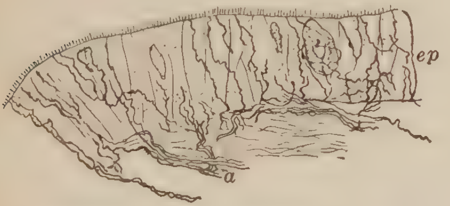

FIG. 94. Free nerve endings in the epithelium of the oesophagus of a frog. After Smirnow.

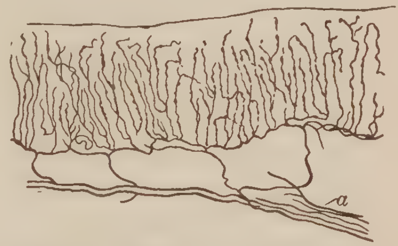

FIG. 95. Free nerve endings in the epithelium of the larynx of a cat. After Cajal.

The **Ruffini endings** occur as large varicose plaques in strands of fascias. Their irregular form is due to the fact that they are embedded in dense connective tissue. They have been found associated with warm spots. Many of the other encapsulated endings such as the Pacinian receptors, cylindrical end-bulbs of Krause and Golgi-Mazzoni receptors, also occur in the deep fascias and ligaments and pressure areas in general and form the deep (protopathic) nerve endings. In the forearm and hand, leg and foot, these endings are supplied by the cutaneous nerves and here a superficial and a deep layer of sensibility are particularly well defined. In other parts of the body the **ligaments** of the various joints receive their afferent supply from adjacent muscular nerves.

Muscle spindles or neuromuscular end organs (figs. 96–98) occur in abundance in all striated muscles, being located near the origin and insertions or tension areas of the muscle. They constitute one of the most extensively distributed, highly organized and functionally important groups of sensory end organs in the muscles of the body. They are long fusiform structures 1 to 4 mm. in length. An outer capsule of connective tissue encloses one or several rudimentary muscle fibers (intrafusal fibers). One or more nerve fibers enter this capsule and end around the intrafusal muscle fibers in spiral ribbon-like branches. The ends of the nerve fibers break up into small discs or flower-like endings. By degenerating the motor fibers, going to a muscle, Sherrington determined that these endings are sensory or afferent in connection. They are found in nearly all skeletal muscles, being most numerous in the small muscles of the hands and feet. They are present in the intrinsic muscles of the tongue. They are found in amphibia, birds and mammals. In the eye muscles of a sheep, R. Krause has shown (fig. 96) a similar but much simpler sensory ending.

Tendon spindles or neurotendinous end organs (fig. 99) occur in tendons and aponeuroses. They are usually supplied by the same nerve that supplies the muscle. In structure they resemble the muscle spindles and on the other hand many transitional forms unite them with the Ruffini endings that occur in fascias and ligaments. The **intrafusal tendon fasciculi** are groups of small tendon fibers surrounded by a capsule of fibrous tissue. The capsule is continuous with the peritendineum. The number of intrafusal fibers varies from 1 to 15 and resemble embryonic tendon. Between the capsule and the intrafusal fibers is a periaxal lymph space. One to three afferent nerve fibers enter the capsule, lose their myelin sheath, and pass between the intrafusal fibers and divide into numerous short twigs which end in clusters of end discs about and between the intrafusal fibers. These end organs are found in all tendons, especially those of the hands and feet. Similar but smaller end organs are found in tendons of extrinsic eye muscles (fig. 96).

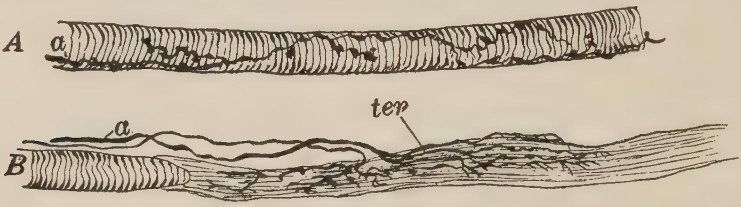

Fig. 96. Simple form of sensory nerve endings in the eye muscles of a sheep. (*A*) ending in tendon, (*B*) ending in muscle. After R. Krause.

The muscle and tendon spindles and sense organs in ligaments are believed to respond to tensions. The afferent impulses they set up provide the organism with deep, bodily, kinesthetic or proprioceptive sensibility, necessary for the maintenance of muscular tonus, propagation of reflex movements and awareness of posture and movement.

Sensory endings in viscera are as a rule much simpler in structure (figs. 94–95). Pacinian receptors occur in the mesentery around some of the large blood vessels in the pericardial region and pleural and peritoneal membranes. Free endings in the form of end brushes or telodendria have been found in the peritoneum and most of the hollow viscera. Various free terminals have been described in the kidneys, pancreas and other organs. Dogiel has shown some forms of these endings in the pericardium and walls of blood vessels. Larsell has demonstrated special endings (fig. 122) in lungs.

The normal mode of stimulation of the receptors is mechanical disturbance or heat and cold. The stimulus probably produces a physical disruption of polarized envelopes that surround the neurofibrillar networks of the terminals. It is not hard to see how such effects would tend to produce a series of successive stimuli. The structure and location of each kind of receptor is probably responsible at least in part for different modalities of sensibilities.

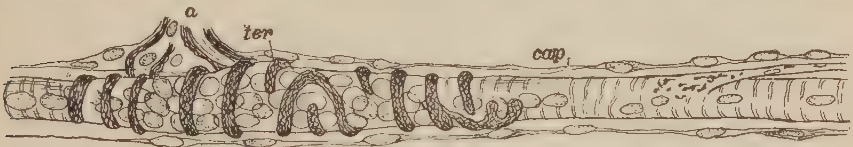

FIG. 97. A simple muscle spindle. After Boeke.

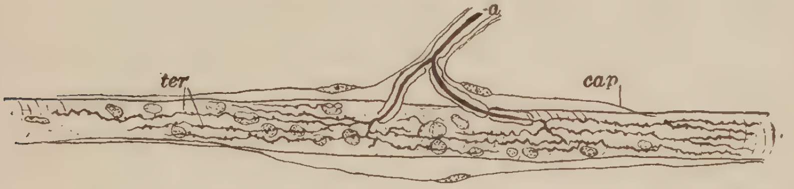

FIG. 98. A simple muscle spindle in the striated muscle of a frog. After Cajal.

A **nerve trunk** should be examined under the microscope. A transverse section of a nerve trunk (fig. 100) is surrounded by a connective tissue sheath, the **epineurium.** Numerous partitions, the **perineurium,** extend into the nerve trunk and divide it into smaller nerve bundles. It is the perineurium that gives the nerve trunks the striped appearance seen in dissections. From the perineurium smaller irregular partitions, the **endoeurium,** extend into the nerve bundles and separate them into still smaller bundles which become the finer **nerve filaments.** The nerve filaments consist chiefly of **myelinated fibers** of the sensory and motor neurones. The central point is the **axone** or **axis cylinder** cut across. Each axone is surrounded by a thick ring, the **myelin sheath,** and external to that a thin connective tissue or neurolemma sheath. Some of these fibers are of small size. These are probably of sympathetic origin and supply the blood vessels and glands in the skin. Other non-myelinated or feebly myelinated fibers are said to be sensory fibers.

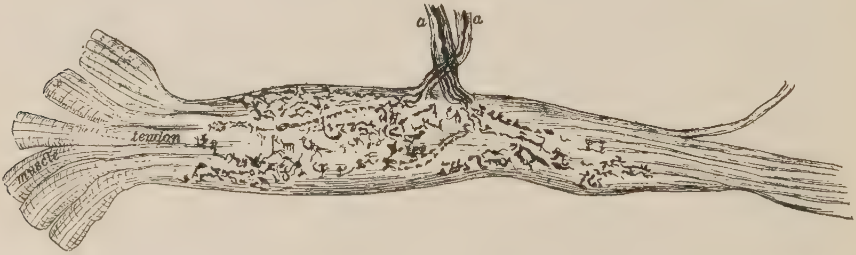

FIG. 99. A tendon spindle. After Ciacio.

The **spinal ganglia** are fusiform or oval enlargements on the dorsal roots of the spinal nerves. They are composed of large and small flask-shaped cells (fig. 103) that give rise to the afferent fibers in the dorsal root filaments and in the peripheral nerves. You have just studied the latter fibers that form the cutaneous nerves and end in specialized receptors in the skin, muscles and viscera. A section of a spinal ganglion examined under the microscope (fig. 102) is seen to be surrounded by a connective tissue sheath continuous with the perineural sheaths. The clusters of large **ganglion cells** are separated by bundles of **nerve fibers.** A closer examination of the cells shows that they contain granular cytoplasm (Nissl granules). These granules are seen best in methylene blue preparations (fig. 103). Each cell contains a large well-defined **nucleus** with a nucleolus. Each cell is surrounded by a connective tissue **sheath** of flat cells. The sheaths are well-defined and the nuclei of their cells stand out prominently. Each cell gives rise by means of an **axone hillock** to a single, stout twisted **axone,** which can be seen best in special preparations (fig. 102). The twistings of the axone are partly around the cell and partly in the capsule of the cell. The tortuosities of the axone take various forms and are spoken of as **glomeruli** though they form no synapses. They can be seen best in intravitam methylene blue or in pyridine silver preparations. Consult the figures of spinal ganglion cells in Dogiel's atlas. Dogiel has classified the cells into eleven types most of which have many characteristics in common. The axone from each cell becomes myelinated, enters the fiber bundles and divides into two, a central or **root fiber** that enters the **dorsal root filaments** and a **peripheral**

fiber, usually larger, **that enters the spinal nerve.** Fibers from the small ganglion cells may be poorly myelinated or non-myelinated. The root fibers of these are said to form the dorsolateral tract of Lissauer (*lis*) in the cord. Their peripheral fibers form a large part of the non-myelinated fibers in the cutaneous nerves and terminate in the free or unencapsulated endings in the skin and elsewhere. These are believed to be the fibers that conduct the impulses of pain. Some of the ganglion cells give off dendritic processes or collaterals from the axone which end on the bodies or axones of other ganglion cells. A small number of nerve fibers enter the ganglia probably from the sympathetic (visceral) rami and terminate in pericellular networks on the ganglion cells (Dogiel).

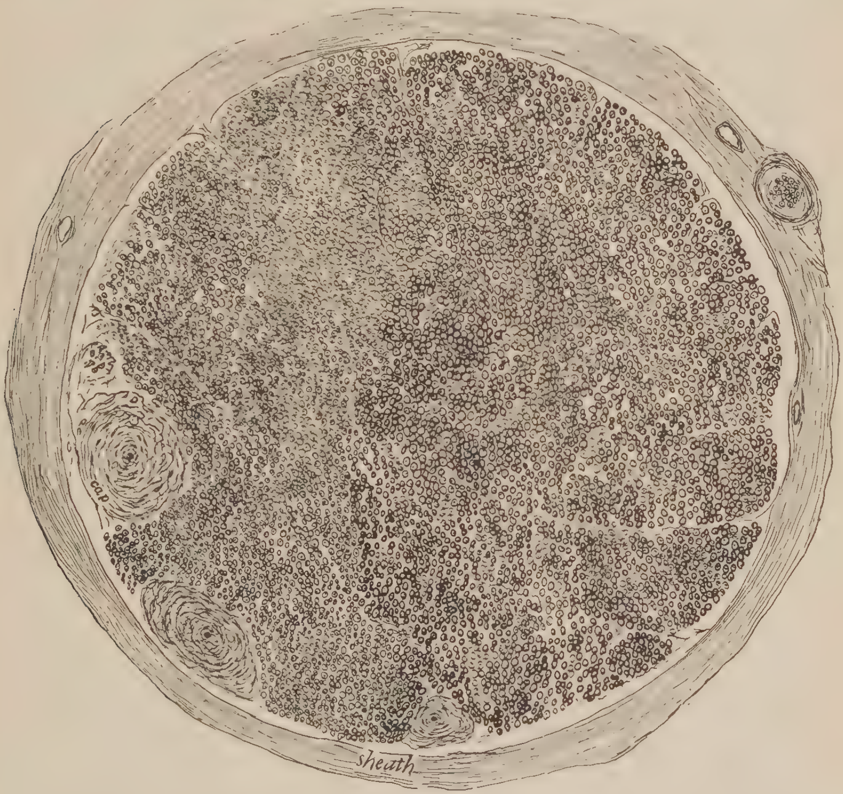

FIG. 100. Cross section of the ulnar nerve of a cat. Note the three Pacinian receptors within the sheath.

Dorsal nerve roots and the **root bundles of the spinal cord** should now be considered. In Nissl sections of a cord examine sections of the dorsal roots. The dorsal root fibers coming from the spinal ganglion cells enter the cord along the dorsal surface of the dorsal gray column. They conduct afferent impulses. Each fiber divides into an ascending and a shorter descending fiber. Figure 104 shows how they end by means of collaterals and end buttons on the cells of the spinal cord. In the dorsal white column these fibers form three definite root bundles (figures 106 and 116): (1) the **dorsolateral tract of Lissauer** (*lis*), (2) the **fasciculus cuneatus** (*fc*) and (3) the **fasciculus gracilis** (*fg*).

Nerve impulse. Living nerve fibers exhibit an electrical potential; and their axones are regarded as being locally polarized for their entire length. Stimuli, such as touch, tension, heat, etc., applied to the sense organs produce a breakdown of this polarity or a wave of negativity which travels along the nerve fiber as a nerve impulse. Its mechanism of production is not understood but may depend on chemical membranes in the nerve fibers. Other properties of nerve impulses are probably due to the organic nature and structure of the axones, embedded as they are in a fluid medium.

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CHAPTER 16

STRUCTURE OF THE GRAY MATTER OF SPINAL CORD

Staining methods for nervous tissue. The **Weigert method** (1884) stains only the myelin sheaths (fig. 106). The tissue is mordanted in one of the chromic salts and stained with haematoxylin. The nerve cells and neuropile stain faintly or may be wholly decolorized. The **Nissl method** stains nuclei and the flakes of tigroid substance in the cells, with warm methylene blue (fig. 107). The **Golgi method** (1873) fills the nerve cells and their processes with a precipïtate of silver rendering them solid black (fig. 108). It tends to select only a few cells or fibers or some groups of these and is therefore a good method for demonstrating the form of nerve cells and their processes as well as cell relations. It is a capricious method. The **Cajal method** is a modification of the Golgi method used to demonstrate neurofibrills and axones. Usually it does not fully impregnate the cells. The **intravitam staining with methylene blue** devised by Ehrlich (1886) colors the nerve cells as well as nerve fibers but fades readily. It is applicable to the demonstration of peripheral end organs, spinal and sympathetic ganglia.

Methods that depend on degeneration of nervous tissue. These are essentially experimental procedures. The **Marchi method** depends on the fact that osmic acid will stain degenerating myelin sheaths and nerve fibers as black dots. Degeneration of these is first produced in the living animal by injury of the fibers or of their cells of origin. The method is applicable to the demonstration of fiber tracts. **Gudden's method** of secondary degeneration depends on the fact that a nerve center and its tracts will fail to develop or will degenerate and atrophy secondarily when an essential part of it is removed. The **clinical pathological method** is similar to Gudden's method. It consists of studying the subjective and objective symptoms of patients and, when they come to post-mortem, studying the location of lesions and the secondary degenerations in their nervous systems. The **chromatolysis method** depends on the fact that after a nerve fiber is injured its cell of origin is liable to undergo degeneration or regeneration, changes which show in the nucleus and cell body. It varies with the degree of injury and the resistance of the nerve cell; but nerve cells can recover from such injury and can regenerate the severed fiber. It is used to demonstrate the cells of origin of motor nerve fibers and of fiber tracts in general, as a supplement to the Marchi method.

Embryologic methods (*His*) show the development of the nervous system differentiation of the nerve cells and of the various centers and tracts. **Flechsig's myelination method** consists of studying the various tracts as they become myelinated in the embryo. He showed that tracts in the central nervous system myelinated at various and definite periods during development. By using a myelin sheath stain it is possible to study the course of tracts that myelinate early.

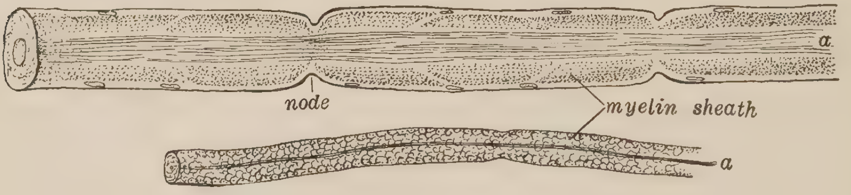

FIG. 101. Longitudinal section of nerve fibers.

The **comparative method** consists of studying the smaller and simpler nervous systems of lower vertebrates and homologizing their various functional mechanisms with those of higher forms, especially the mammals. It employs all of the preceding methods.

Structure of the gray matter of the spinal cord

For this study a microscope and drawing material should be provided and sections stained by the Weigert and Nissl methods should be examined. Satisfactory Golgi, Cajal and Marchi sections are harder to get, so these will be demonstrated only as they are available. In order to understand how the minute structure of the central nervous system has been established, these and various other methods not readily applicable in a laboratory will be briefly explained.

Sections of the cord through the cervical, thoracic and lumbar regions stained by the Weigert, Nissl and Cajal methods should be studied under the microscope (figs. 106 to 108). Note that the pia forms a fibrous sheath for the cord and sends into its substance many strands. The **ventral fissure** (*vf*) is formed by an infolding of the pia. Where the nerve roots are present the pia passes onto them, and large blood vessels are seen in the **vascular tunic** of the cord. The **dorsal septum** (*ds*) and the **ventral fissure** almost divide the cord into lateral halves. Like the body, the cord is bilaterally symmetrical.

The **gray substance of the spinal cord** consists of nerve cells embedded in a feltwork of fine fibers or neuropile (fig. 106). See Bruce's atlas and article by Jacobsohn. Examine sections through the thoracic, lumbar and cervical regions of the cord stained by the Nissl method (figs. 107 and 109). The gray matter is disposed in the form of an *H* enclosed on each side by the three white columns which in Weigert sections stain very darkly. The middle transverse piece is the **gray commissure** (*cg*) in the center of which you will find the **central canal** (*c*). The lateral portion is divisible into (1) a broad **ventral gray column** or ventral horn (*vh*) of efferent or motor cells which give rise to the efferent fibers in the spinal nerves and (2) a narrow **dorsal gray column** or dorsal horn (*dh*) on which fibers of the dorsal (afferent) nerve roots (*dr*) and collaterals (*k*) from the fibers of the fasciculus cuneatus (*fc*) and fasciculus gracilis (*fg*) terminate. The dorsal column (*dh*) consists of receptive cells (figs. 107, 108, *sg* and *cen*) which serve as a nucleus of termination for the afferent fibers of the spinal nerves. In cross sections the dorsal and ventral columns are spoken of as **dorsal horn** (*dh*) and **ventral horn** (*vh*). Only a small part of the information for the understanding of the cord can be derived from ordinary sections, so atlases and books must be used to supplement them.

The dorsal horn

The **dorsal horn** in size is said to correspond with the sensory field of distribution of the dorsal roots and inversely to the length of the cord segment. Thus the long thoracic segments have a very narrow or short dorsal horn. Connecting its point with the outer surface is Lissauer's tract (*lis*) consisting of fine myelinated dorsal root fibers. Numerous fine fibers or collaterals (*k*) pass into the dorsal horn from the fasciculus gracilis (*fg*), fasciculus cuneatus (*fc*) and from the dorsal nerve root (figs. 104 and 110). Very small nerve cells make up the dorsal gray column. In Weigert sections (fig. 106) they form a clear, often folded area, the **substantia gelatinosa** (*sg*). The form and connections of these cells is shown best in silver preparations (fig. 108). Numerous collaterals pass into the substantia from the overlying root fibers (fig. 110, *dr*) and Lissauer's tract (*lis*) best seen in Weigert section. It must be appreciated that the substantia forms a long fluted column that extends the entire length of the cord and receives an abundance of collaterals from the entering dorsal roots of the spinal nerves. Hence it is regarded as the proper sensory nucleus of the cord (fig. 109). There is evidence that cutaneous sensibility in particular is discharged into the cells of the substantia.

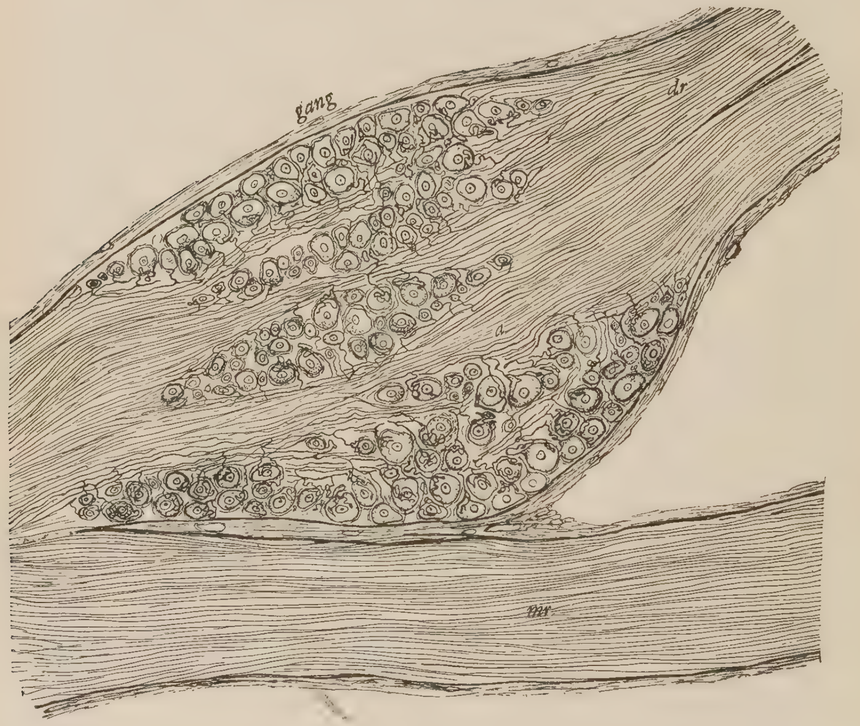

FIG. 102. Section of a spinal ganglion of a cat. Pyridine silver method.

The substantia (*sg*) covers over and encloses an area of fine fibers (*cen*), seen best in Weigert sections, containing some fine cells like those of the substantia and a few medium sized cells. The whole area (*cen*) is very characteristic in appearance and always related both in size and disposition to the substantia. It is spoken of as **Waldeyer's nucleus,** and the large cells get the name of **central nucleus.** It has been shown by Cajal that the cells of the substantia as well as those in Waldeyer's nucleus send their axones into the fasciculus proprius that surrounds the dorsal horn (fig. 108). They probably conduct thermal (pressor and depressor) and painful sensibilities (Ranson). The large cells that form the **central nucleus** (*cen*) send their fibers into the lateral columns of the same and of the other side (fig. 108). It seems likely that they are concerned with the conduction of tactile sensibilities upwards to the brain-stem and thalamus (spino-thalamic) tracts. Experimental cutting of the ventrolateral side of the cord tends to abolish cutaneous sensibility below the level of the cut (Frasier).

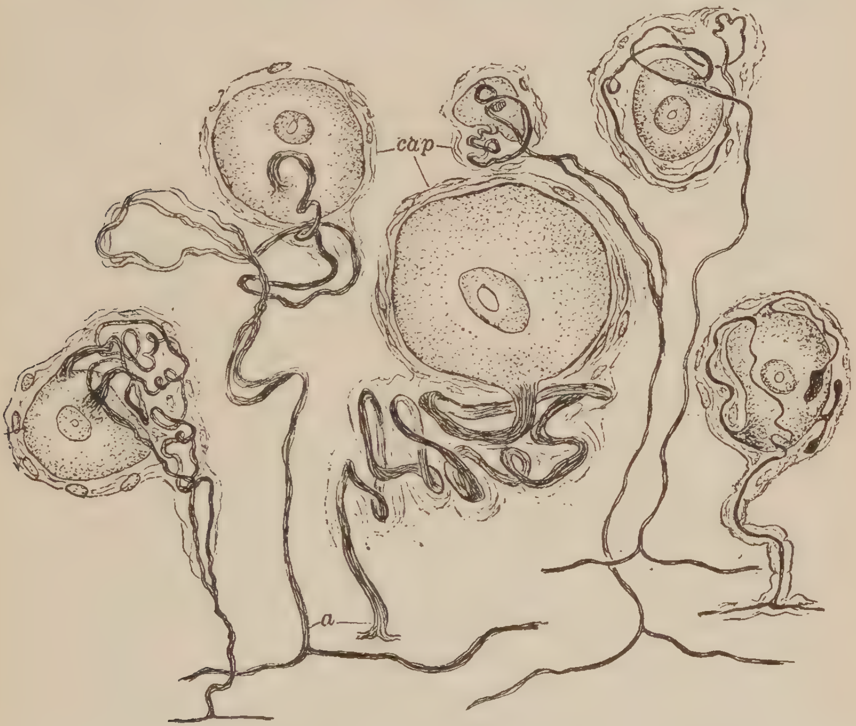

FIG. 103. Spinal ganglion cells, methylene blue stain. After Dogiel.

The narrow intermediate part of the dorsal gray column is known as the **neck.** Where the column broadens to join the ventral gray column and gray commissure it possesses a cluster of large cells in its dorsal side. This is the **dorsal nucleus** or column of Clarke (fig. 108, *dn*). It extends from the upper lumbar segments through the entire length of the thoracic portion. It stands in intimate relations to the fasciculus gracilis (*fg*) which sends numerous collaterals into it (fig. 110). These are best seen in Weigert and in silver sections. It has been shown that cells of the dorsal nucleus (of Clarke) give origin to the dorsal spino-cerebellar tract (Flechsig) of the same side (fig. 114, *dsc*). For if the tract is cut or injured the nucleus degenerates below the level of injury and vice versa. It has been shown that the nucleus gives origin also to the crossed ventral spinocerebellar tract of the other side. It is probable that proprioceptive impulses are sent by these tracts into the cerebellar cortex (vermis). Since marked motor disturbances are associated with the degeneration of these nuclei and tracts they are believed to conduct exclusively deep or muscular sensibility to the cerebellar cortex. (See pages 209 and 266.)

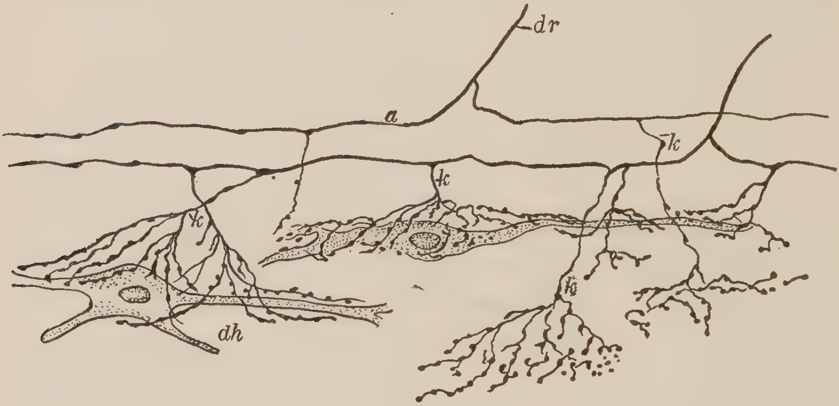

Fig. 104. Terminals of dorsal root fibers on cells of spinal cord. After Cajal.

The **intermediate nucleus** (*in*) of Cajal (figs. 107–108) is a large group of small cells situated in the center of each gray column opposite the gray commissure. Several groups are recognized in this nucleus. The largest is the **intercornual,** so-called by Jacobsohn (fig. 109) because it lies on the lateral side between the ventral and dorsal horns. By Cajal it is called the nucleus of the lateral column (*nlf*). The **mediodorsal** group surrounds the dorsal nucleus of Clarke. The **ventromedial group** (*in*) is in the interior of the ventral horn. These groups are especially large in the cervical and lumbar enlargements, associated in part with the increase in size of the ventral horn. In Weigert and silver sections these nuclei (*in* and *nlf*) are seen to receive a large number of collaterals from the dorsal root zone, that forms the lateral half of the fasciculus gracilis (figs. 110 and 115). The cells of these nuclei are small, but widely branching. They give off axones that form the large fasciculi proprii (reflex tracts) that surround the ventral horns of both sides (fig. 114, *lp*, *vp*). From the intermediate nucleus (*in*) a large number of these fibers cross (fig. 108) and form a prominent ventral commissure (*vc*) and ventral fasciculus proprius of the cord (*vp*) seen especially well in the cervical enlargement. For this reason the intermediate nucleus is also called the commissural nucleus. The intercornual nucleus or nucleus of the lateral column (*nlf*) gives rise to fibers that surround the lateral and ventral sides of the ventral horn and are known as the lateral fasciculus proprius. In "spinal animals" the fasciculi proprii or reflex bundles remain intact. In such animals the reflex (motor) functions of the cord have been studied extensively by Sherrington. It is believed that the nucleus intermedius and fasciculi proprii are an essential part of the spinal mechanism for integration of spinal reflexes. It is known that the fibers of the fasciculi proprii terminate on the motor cells of the ventral horn and there is some evidence that the cerebrospinal tracts end on the cells of the intermediate nucleus (intercornual group) and not directly on the motor ventral horn cells. The distribution of the intercornual, dorsomedial and ventromedial group of cells in the different segments of the human cord are best seen in Jacobsohn's figure 109.

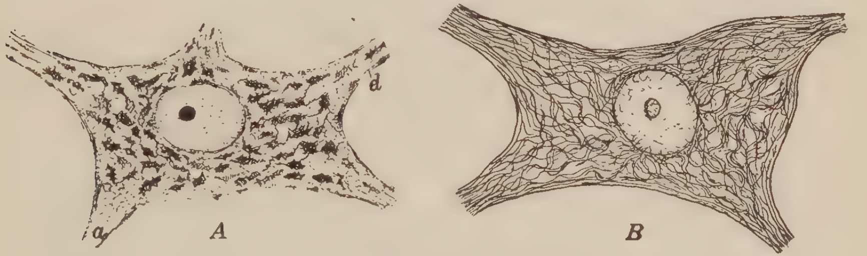

FIG. 105. Motor cells of ventral horn, highly magnified. (*A*) Nissl stain; (*B*) neurofibrillar stain.

The ventral horn

In a section through the thoracic cord (fig. 106) the ventral horn is simple. In the **ventral gray column** can be seen the **ventromedial** and **ventro-lateral groups** of large cells. These are motor cells that send their fibers into the ventral roots of the spinal nerves to supply skeletal muscles. They are found in every segment of the cord. It is thought that the ventromedial group supplies the long muscles of the back and neck (sacrospinalis) and that the ventrolateral group supplies the intercostal muscles and muscles of the abdominal wall (van Gehuchten). The large motor cells (fig. 108) are seen in silver preparations to branch widely and their axones give off collaterals before they leave the cord. At the base of the **ventral gray column** and on its lateral side is a small **lateral gray column** or lateral horn (fig. 118, *lh*). The cells of this column contribute (preganglionic) fibers that pass through the white rami communicantes and terminate on cells of sympathetic (visceral) ganglia (fig. 118). This sympathetic column of cells is absent in the cervical region. It is prominent in the thoracic region where it gives rise to the cervical sympathetic chain, the cardiac plexus, white rami communicantes of the intercostal nerves and the splanchnic nerves. It appears again in the lower sacral segments that supply the hypogastric plexus. Follow this column through the thoracic segments in Bruce's atlas or in Jacobsohn's figures.

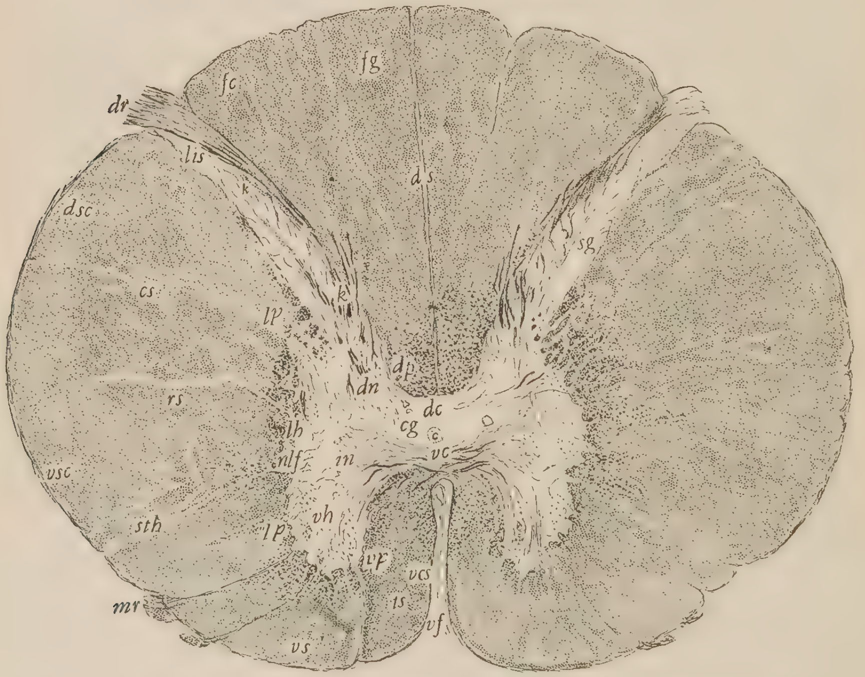

FIG. 106. Section of 8th cervical segment of the human cord. Weigert stain, × 10.

Sections through the cervical and lumbar enlargements (figs. 107 and 109) show a great increase in size of the ventral horn. In addition to the ventro-medial column seen in the thoracic region, a great **lateral cell column** appears which is subdivided into a ventral lateral group, a dorso-lateral, a central and a retro-dorsal. These have an evident relation to the increase of the motor roots of the brachial and lumbo-sacral plexuses. The groups extend through several segments. For segmental distribution of these groups see van Gehuchten, p. 477, or Quain, p. 77. A study of atrophy of these groups following amputation (van Gehuchten, Marinesco, Sano) has shown that these cell groups supply groups of muscles which ordinarily act together. It appears that the dorsolateral groups supply the muscles of the hand and forearm, the lateral group, muscles of the arm and the central group muscles of the breast and shoulder. In the lumbo-sacral region of the cord the medial groups of cells are regarded as supplying the vertebral and abdominal muscles. The lateral groups supply the muscles of the leg and the central and dorso-lateral the muscles of the foot.

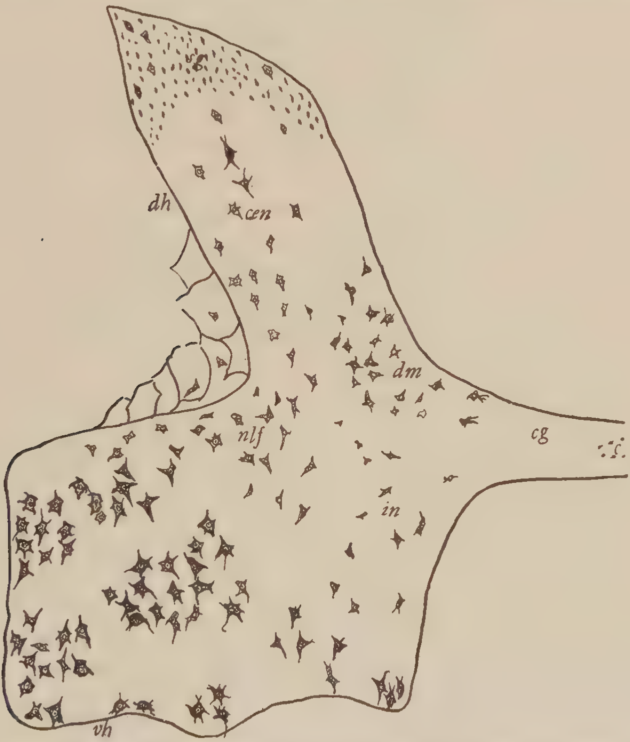

FIG. 107. Section of left half of gray column of the cervical cord of man. Nissl stain, showing cell groups. After Jacobsohn.

The individual skeletal muscles are differentiated by their position, origin, insertion, unity of mass; and several (synergists) may have a common action. They are grouped into agonists and antagonists, groups having opposing actions, as flexors versus extensors or pronators versus supinators. The number of cell groups in the cord is likewise much smaller than the number of muscles. It appears that these cell groups supply groups of muscle which have a unity of action or whose actions are integrated (added together) to perform common movement.

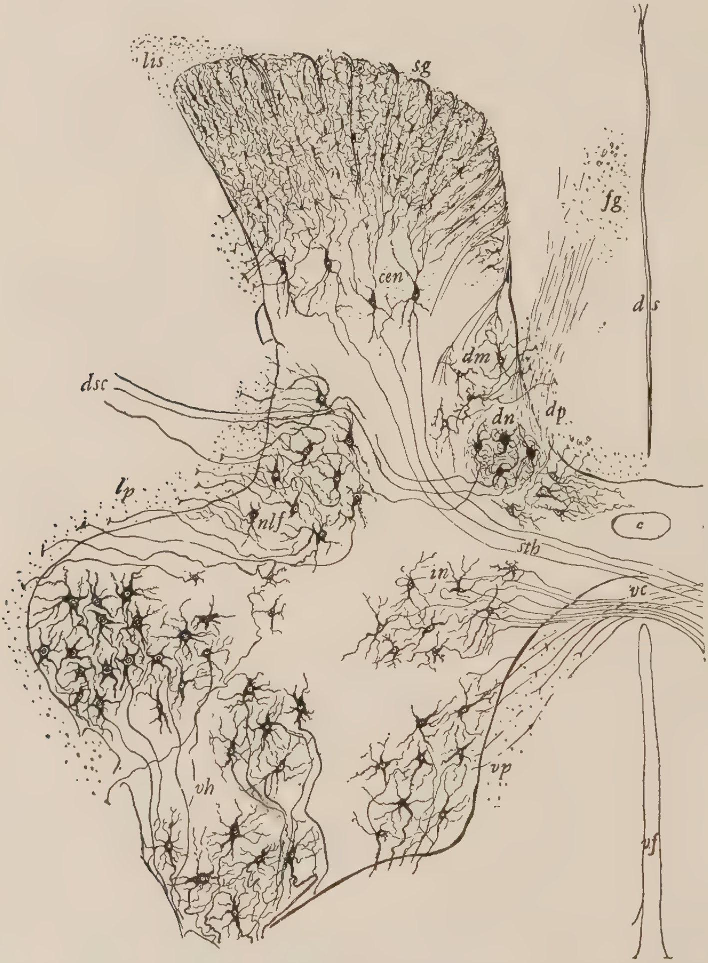

FIG. 108. Schematic section of one half of the lumbar cord of man showing cells. Silver stain.

Connections of the motor cell groups (fig. 110). Weigert and silver sections show a large number of collaterals streaming into the ventral horn from the surrounding white matter as well as from the dorsal columns. (1) That long **reflex collaterals** (*k*) connect the dorsal root zone (*dr*) with the motor groups has been shown by Cajal (fig. 110) from which it appears that direct reflex connections exist between the dorsal and ventral nerve roots. This forms a two neurone arc. (2) The fasciculi proprii (*vp* and *lp*) which sur-

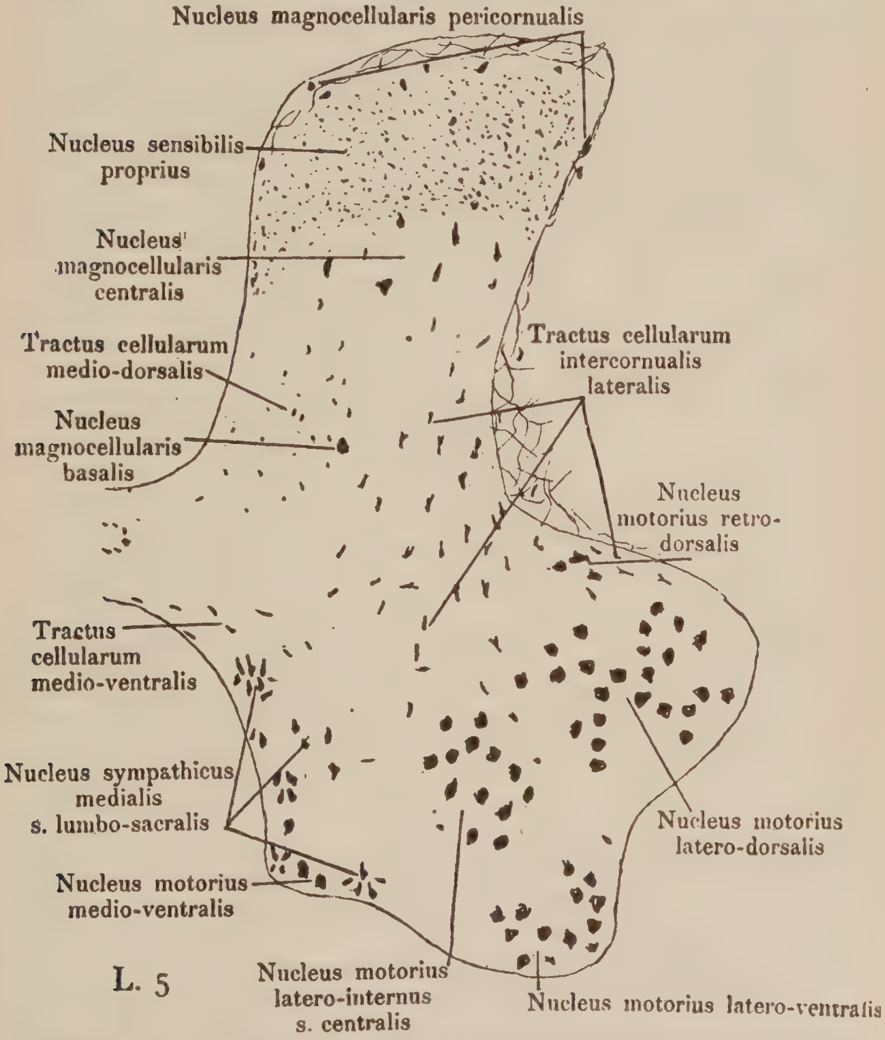
Nucleus magnocellularis pericornualis
Nucleus sensibilis proprius
Nucleus magnocellularis centralis
Tractus cellularum medio-dorsalis
Nucleus magnocellularis basalis
Tractus cellularum intercornualis lateralis
Nucleus motorius retro-dorsalis
Tractus cellularum medio-ventralis
Nucleus sympathicus medialis s. lumbo-sacralis
Nucleus motorius latero-dorsalis
Nucleus motorius medio-ventralis
L. 5
Nucleus motorius latero-internus s. centralis
Nucleus motorius latero-ventralis

FIG. 109. Nuclear masses in the 5th lumbar segment of man. After Jacobsohn.

round the ventral horn send into it great quantities of collaterals which do not degenerate in " spinal animals." These connections through the intermediate nuclei (*in* and *nlf*) and fasciculi proprii may be looked upon as one of the chief integrating mechanisms which connects the dorsal (sensory) and the ventral (motor) roots. This is a three neurone arc. (3) Numerous other collaterals from the ventral and lateral columns enter the ventral horn (fig. 110) which degenerate when the vestibulospinal and other descending tracts are cut at higher levels. The cerebro-spinal tracts and other tracts may end on the intermediate nucleus. The mode of termination in all cases is in the form of a dense brush work (fig. 110) and terminal buttons (fig. 111) which occur in great numbers on the surface of the cell bodies.

The motor nerves are formed by the fibers given off by the large multipolar cells of the ventral horn (figs. 82 and 105). These fibers constitute about three-fifths of the muscular nerves that enter ordinary striated muscles. As they enter the muscle each fiber begins to branch extensively, giving rise to a large number of terminals each of which reaches a single muscle fiber, penetrates the sarcolemma and forms a **motor end plate.** This is also spoken of as a neuromuscular junction. Such motor end plates are shown in figures 112 and 113. By means of the silver method it has been shown that these nerve terminals are expansions of the neurofibrillar network of the motor axone (fig. 113). This network stands in relation to the muscle fibrils by means of the periterminal network of Boeke (fig. 113) which has the nature of protoplasmic condensations in the sarcoplasm.

Reflex arcs and synaptic functions

The **neurone** is the anatomical unit of the nervous system; the **reflex arc** is the physiological unit. The sensory and motor nerve fibers serve as two way conductors of nerve impulses between the cord and the periphery. Within the cord and brain-stem the sensory and motor nerves enter into functional connections whereby the sensory fibers can set up impulses in the motor nerves.

There is no functional or anatomical *continuity* between the neurones; but the neurones of one limb of the arc enter into close *contact* with the cells of the other limb. These contacts are in the nature of terminal buttons (figs. 104 and 111) which occur in large numbers on the cell bodies and their dendrites. Impulses in the afferent nerves are thus able to impinge on the surfaces of other cells in the gray matter of the cord and excite or inhibit their activity. These physiological relations are called synapses. They provide the mechanism for **synaptic** or interneuronal **conduction.**

This exhibits the following properties:

1. Excitations or inhibition of the activities of the cell.
2. Summation of ineffective stimuli takes place; and an algebraic summation of stimuli brought to the surface of the cell by fibers from several sources.
3. Facilitation or induction or susceptibility to other stimuli previously too weak or ineffective.
4. Irreversibility, conduction is from buttons to the cell.
5. Fatigue occurs and makes synaptic conduction less active.

All reflex acts require three types of conduction: (*a*) conduction through the nerve fibers (see page 156), (*b*) conduction through the synapses and (*c*) conduction through motor terminals.

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CHAPTER 17

STRUCTURE OF THE WHITE SUBSTANCE (TRACTS) OF THE CORD

Minute structure of the white columns and nerve roots. With the higher powers of your microscope examine Nissl (fig. 107) and silver sections of the spinal cord; identify on the outside the thick fibrous **dura mater.** Examine the arachnoid and the **pia,** the **nerve roots.** Study the dorsal, lateral and ventral white columns. The myelin has been largely dissolved out of the sheaths. Examine the nerve roots with the high power. They are cut transversely. Each small ring is a **nerve fiber** cut across. In the center find the deeply stained **axone,** or **axis cylinder.** The clear ring around the axone is the **myelin sheath** which has been largely dissolved away. The peripheral or outer ring deeply stained is the **neurolemma sheath** and its nuclei. For lettering on figures see page xxi.

Now examine the dorsal, lateral and ventral columns of the cord. The deeply staining dots are the **axones** enclosed by a clear ring, the dissolved **myelin sheath.** The **neuroglia** forms the more delicate outer rings which enclose the myelin sheaths. Note that the **neurolemma** or connective tissue sheaths are absent from these fibers in the central nervous system. Note the difference in size and distribution of the nerve fibers. How do the fibers in the dorsolateral tract of Lissauer (*lis*) and in Waldeyer's nucleus (*cen*) compare with those of the fasciculus cuneatus (*fc*) and gracilis (*fg*)? Note the numerous **collaterals** (*k*) and **nerve fibers** that pass between the white columns and the gray columns. Note the streams of elongated nuclei of the neurolemma on the outgoing ventral roots.

Fiber tracts of the cord

The white matter of the cord is divisible into (1) the dorsal, (2) the lateral and (3) the ventral white columns or funiculi of each side. In this order they should be studied in the cervical, thoracic and lumbar portions of the cord on Weigert and Nissl sections (figs. 106, 114).

In ordinary sections only the three columns are evident. Special preparations are necessary to demonstrate the tracts in a degenerated condition. Tumors, locomotor ataxia, myelitis and apoplexy will cause degeneration of some of the tracts. The cord of a newborn babe will show different stages of myelination. See demonstration specimens.

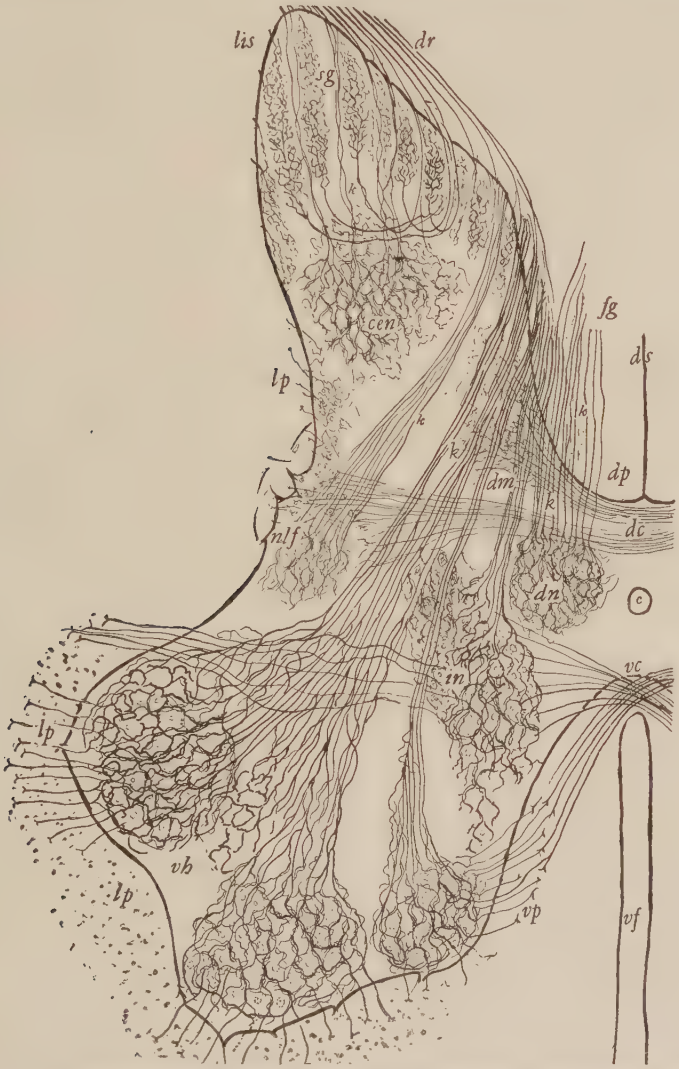

FIG. 110. Schematic section of cord in which the collateral connections of the various groups of cells are represented. Compare with figures 107 to 109.

The **dorsal white column** on each side of the septum (*ds*) presents a triangular outline in cross section. Its deep surface is bounded by the dorsal horn into which it sends many fine fibers or **collaterals** (*k*). The portion near the dorsal septum is the **fasciculus**

gracilis (*fg*). This is formed by the **ascending dorsal root fibers** (*dr*) **of the sacral, lumbar and thoracic nerves.** The lateral portion in the cervical region is the **fasciculus cuneatus** (*fc*). This is formed by the **ascending dorsal root fibers of the upper thoracic and of the cervical nerves.** The **dorso-lateral fasciculus** (of Lissauer) will be seen as a fine stippled bundle (*lis*) overlying and invading the tip of the dorsal horn. It is also a **dorsal root bundle** composed of fine myelinated fibers. The point of entrance of the **dorsal root filaments** (*dr*) is always over the tip and dorsal surface of the dorsal horn. The lateral portion of their root fibers being contributed to the dorso-lateral fasciculus (*lis*) and the medial to the fasciculus gracilis (*fg*) and cuneatus (*fc*). In any section the entering dorsal roots form a **root zone** over the dorso-medial side of the dorsal root. The long ascending fibers that form the fasciculi gracilis (*fg*) and cuneatus (*fc*) are always medial to this root zone.

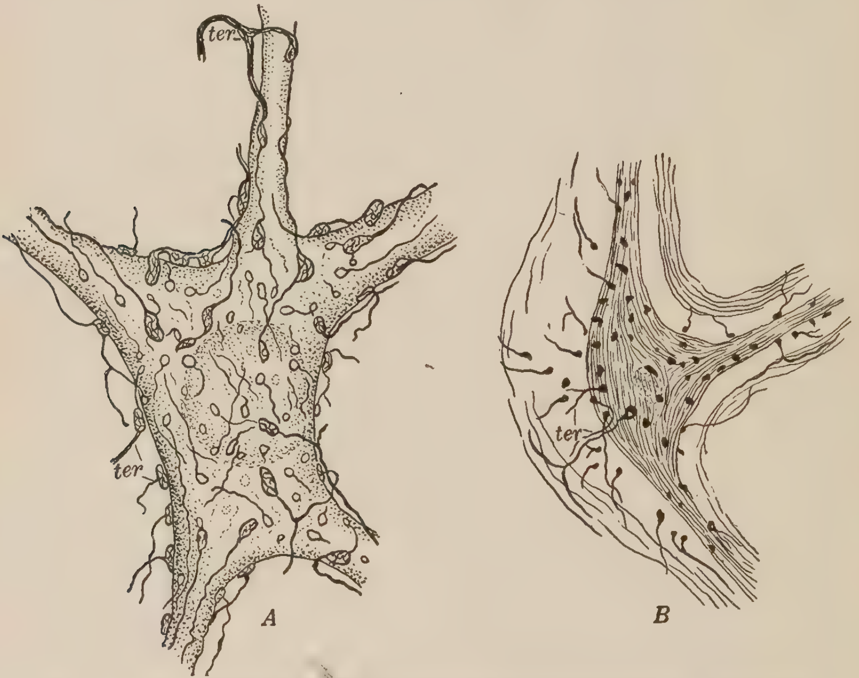

Fig. 111. (*A*) Terminal end buttons on a motor cell of the cord. After Cajal. (*B*) Terminal end buttons on a reticular cell. After Van Gehuchten.

The origin and course of the long fibers of the fasciculus gracilis are demonstrated by lesions of the long dorsal roots that form the cauda equina, lesions such as tumors, locomotor ataxia or experimental section of these roots in an animal (see demonstrations). Likewise cutting any of the dorsal cervical roots degenerates the fasciculus cuneatus (*fc*). Flechsig and Trepinski demonstrated the root zone and fasciculi by the myelination method in fetuses. The general arrangement of the fibers in these dorsal fasciculi is such that the long root fibers of the sacral nerves occupy a position near the median septum, the lumbar occupy an intermediate position and the thoracic a lateral position in the fasciculus gracilis (*fg*). In the cervical region the long ascending root fibers of the cervical nerves form the **fasciculus cuneatus** (*fc*) which occupies a position lateral to the fasciculus gracilis. This arrangement applies to the long root fibers that ascend the whole length of the cord, but not to the root zone, for some of its fibers terminate in the gray matter at different levels for the purpose of effecting reflex connections. The **dorso-lateral fasciculus** (of Lissauer) is composed of short root fibers for the most part and remains small and maintains a position over the tip of the dorsal gray column where these root fibers enter. In the upper cervical region its place is taken by the descending root of the trigeminus nerve.

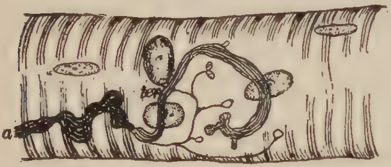

FIG. 112. Motor end plate in striated muscle of hedgehog. After Boeke.

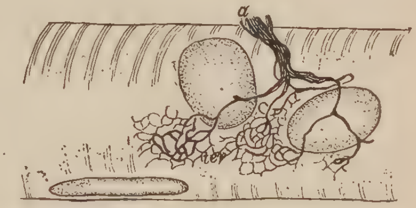

FIG. 113. Motor end plate in striated muscle of a bat. After Boeke.

Collaterals are short twigs by means of which the fibers of the white substance **make connections** with cells of the gray matter (figs. 110 and 115). Note the great number of dorsal collaterals; these are fine twigs that branch from the root fibers in the dorsal fasciculi and enter the dorsal horn and intermediate nucleus where they terminate around the cells. The collaterals from the dorso-lateral fasciculus (of Lissauer) stream through the substantia gelatinosa (*sg*) and end on its cells or on the cells in Waldeyer's nucleus (*cen*). The fine fibers seen in this nucleus are collaterals as well as axones that run short distances and connect different levels of the substantia. In the thoracic region collaterals from the **fasciculus gracilis** terminate in the dorsal nucleus (*dn*) at the base of the dorsal gray column. Others from the root zone terminate on cells in the intermediate nucleus (*in*). Other longer collaterals pass into the ventral gray column; these are known as the **direct reflex collaterals** since they discharge the efferent impulses directly into the motor cells.

The **dorsal fasciculus proprius** (*dp*) is a small bundle of fibers scattered among the fibers of the dorsal column, concentrated chiefly on the dorsal surface of the dorsal gray column. It gets its name from the fact that its fibers are derived from the cells of this column and are limited to the cord. They probably mediate some of the intersegmental reflexes or sensibility.

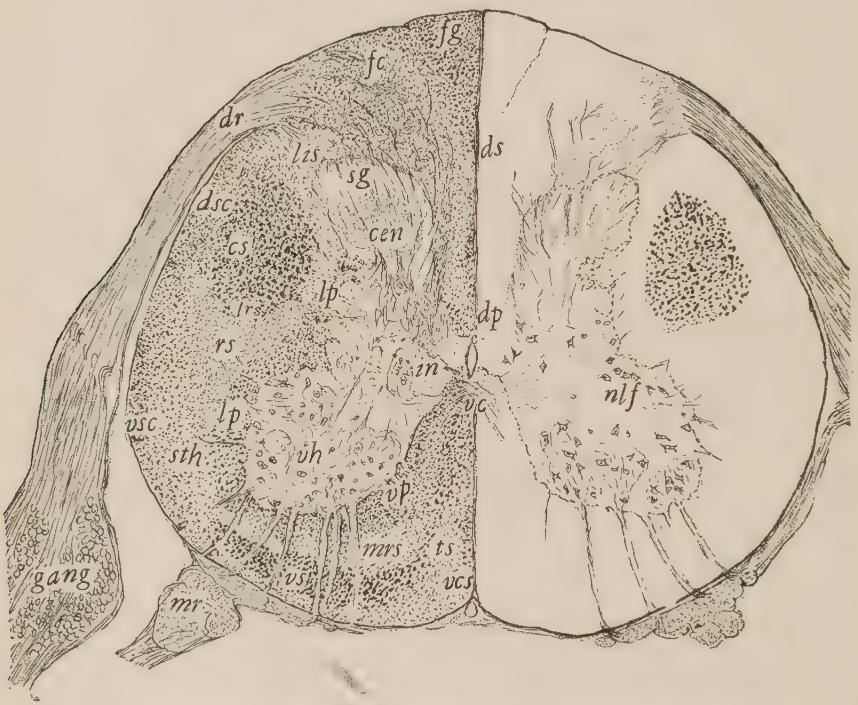

FIG. 114. A transverse section of the 7th cervical segment of the cord of a cat, showing position of various tracts. Marchi method, × 12.

The **lateral white column** of the cord (*lco*) on each side presents an oval outline. Its medial surface is bounded by both dorsal and ventral gray columns. On its medial surface it is invaded by the intercornual group (*nlf*) of the intermediate nucleus, so that a number of small bundles are enclosed by the gray; this forms the **reticular formation** of the cord. The lateral white column is divisible into several topographical areas which have important functional significance (fig. 114). The area of fibers concentrated along the lateral surfaces of the dorsal and ventral gray column is the **lateral fasciculus proprius** (*lp*) of the cord (fig. 116). The dorsal part is probably a sensory conduction system. These fibers take origin from the cells in the dorsal gray columns and are limited to the cord. The ventral part is derived chiefly from the intercornual nucleus (*nlf*) and is a reflex bundle. With the dorsal and ventral fasciculi proprii it forms the most primitive and fundamental fibers of the cord whose purpose it is to connect the various cord segments for appropriate intersegmental reflexes.

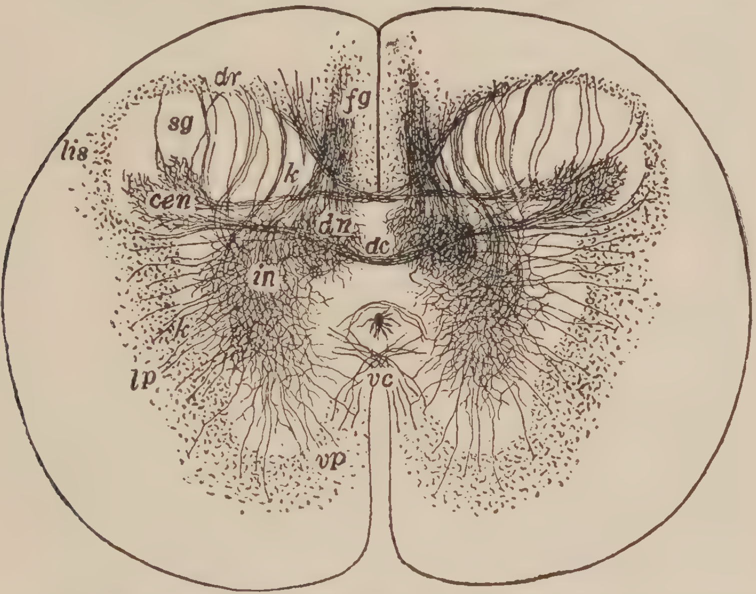

FIG. 115. A transverse section of the thoracic cord of a foetal calf, showing collaterals into gray matter, silver method. From Van Gehuchten.

Lateral to the dorsal gray column is a large round area of fibers (*cs*) formed by the **lateral cerebro-spinal tract** (or lateral pyramidal tract). It is best shown in the cord of a new-born babe in which it is not yet myelinated. It is separated from the dorsal horn by the lateral fasciculus proprius and reticular area. The fibers of the lateral cerebro-spinal tract (*cs*) have their origin in the precentral gyrus (2, 4) of the cerebral cortex. They are very long fibers that descend through the internal capsule, peduncles, pons, oblongata and the whole length of the cord. Their crossing occurs at the lower level of the oblongata. They discharge motor impulses of an adaptative nature that originate in the cerebrum into the intermediate nucleus or into the motor cells of the cord. As this is one of the most important bundles in the cord its position should be ascertained as well as possible (fig. 114, *cs*).

Just lateral to the lateral fasciculus proprius and ventral to the crossed cerebro-spinal tract is the **rubro-spinal tract** (*rs*). It is best demonstrated in the cord of an animal in which the tract has been cut in the lateral side of the oblongata (Monakow) and has been allowed to degenerate. Its fibers arise from the opposite red nucleus in the midbrain (mesencephalon) and end on cells in the ventral horn (fig. 152). Between the foregoing tracts and the lateral fasciculus proprius there is an **intermediate fiber zone** where the fibers of the various tracts are mixed with each other and those of the fasciculus proprius as they enter or leave the various segments of the cord.

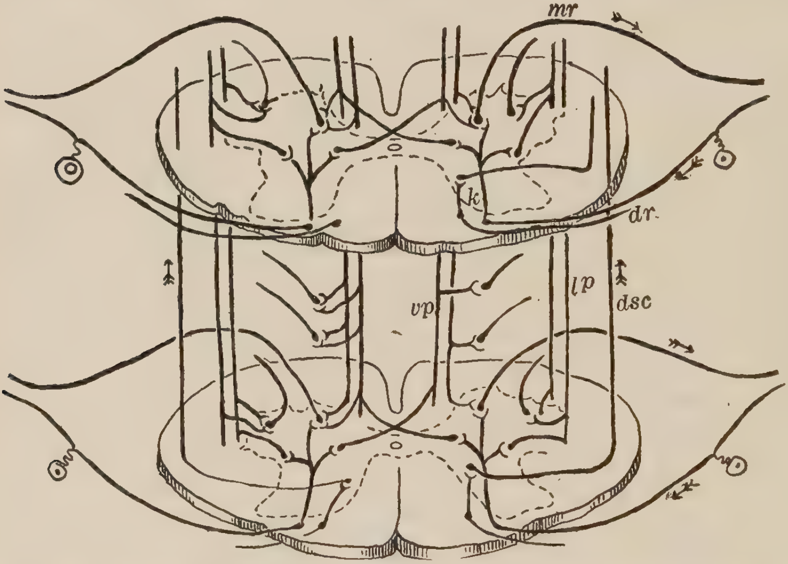

FIG. 116. A schema to show the origin and course of the fasciculi proprii and the dorsal spinocerebellar tracts.

On the lateral surface of the cord lateral to the cerebro-spinal tract and dorsal horn is a flat band of fibers (*dsc*) the **dorsal spinocerebellar tract** (of Flechsig). It arises from the cells of the dorsal nucleus (*dn*) of the same side (figs. 108 and 116) and extends up to enter the cerebellum by way of the restiform body. Its fibers end chiefly in the cortex of the cerebellar vermis, in the nodulus, uvula pyramis. On the ventro-lateral surface is the **ventral spino-cerebellar tract** (*vsc*). This arises from cells in the basis of the dorsal columns of both sides. Its origin is said to be also in cells of the dorsal nucleus of Clarke, but the exact location of its cells of origin is uncertain. It enters the cerebellum by way of the brachium conjunctivum. Its fibers end in the upper part of the cortex of the cerebellar vermis, that is in the culmen and central lobule.

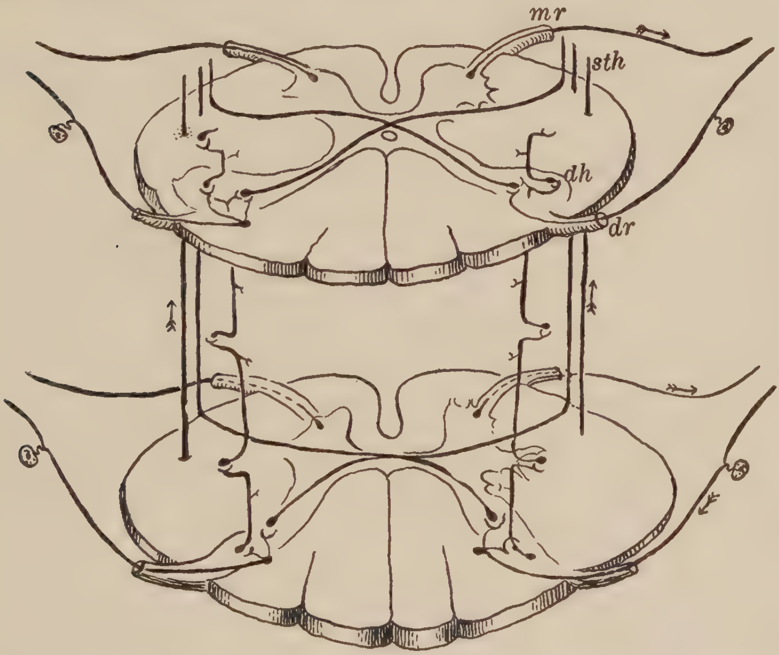

Fig. 117. A schema to show the origin and course of the crossed spino-thalamic tracts and the chaining of the neurones of the substantia gelatinosa.

Between the rubro-spinal tract and the ventral spino-cerebellar tract and mingled with the latter is another flat bundle, the lateral **spino-thalamic tract** (figs. 114 and 117, *sth*). Its fibers arise from cells in the opposite dorsal horn for the entire length of the cord and extend upward and end in the **lateral nucleus** of the oblongata (fig. 129, *ln*). From here fibers ascend and end in the lateral nucleus of the thalamus. This system of spino-thalamic fibers (*sth*) conducts cerebralward the impulses of pain, heat and cold. In the brain-stem they shift dorsally into the reticular formation and join the central tegmental fasciculus (*cf*).

In the region of the outgoing ventral nerve root is the **ventral spino-thalamic tract** (fig. 117, *sth*). It arises from cells in the opposite dorsal gray column along the whole length of the cord. In the brainstem it joins the medial lemniscus and passes up to terminate in the lateral nucleus of the thalamus to which it conducts impulses of touch and pressure. Its lateral and more superficial fibers are mixed with the ventral spino-cerebellar tract of Gowers in which it was formerly included. As seen in figures 110 and 115 a system of collaterals joins the dorsal horns. These are derived partly from dorsal root fibers and in part from dorsal horn cells and surrounding fibers. This arrangement may account for the bilateral conduction of pain and other sensibilities.

The **ventral white column of the cord** (*vco*) of each side borders the ventral gray column (*vh*) on its ventral and medial sides. Laterally it is perforated by the ventral root filaments and on the medial side it is bounded by the ventral fissure (*vf*). It is composed of a number of tracts. Bordering the ventral fissure and extending along the ventral surface as a flat band of fibers is the **tecto-spinal tract** (fig. 114, *ts*). Its fibers arise from the superior colliculus of the midbrain and end on cells of the ventral gray column. It is a visual reflex tract. Lateral to it is a larger tract, the uncrossed or **ventral cerebro-spinal tract** (*vcs*). This has the same origin and termination as the crossed cerebro-spinal tract. Adjoining it is the crossed **vestibulo-spinal tract** (*cvs*). Its fibers arise from the medial vestibular nucleus and terminate on cells in the ventral horn (fig. 150). Ventral to the ventral horn on the surface of the fasciculus proprius (*vp*) is the **direct vestibulo-spinal tract** (*vs*). Its fibers arise from the lateral vestibular nucleus (Deiters') in the oblongata and descend to terminate on the cells of the ventral horn. Between this tract and bordering the ventral and medial surface of the ventral horn is the **ventral fasciculus proprius** of the cord (fig. 116, *vp*). Its origin is from cells in the intermediate nucleus and its fibers end on cells of the ventral horn.

In the cervical region the fasciculi proprii end in relation to the ventral medial and dorsal (accessory) olivary nuclei. These in turn connect with the cerebellar vermis by olivo-cerebellar fibers. Between the ventral fasciculus proprius and the other ventral bundles is the **medial reticulo-spinal tract** (*mrs*) coming from the large cells of the gray reticular formation of the medulla oblongata (*bulb*) and pons and ending on cells of the ventral gray column. A **lateral**

reticulo-spinal tract (*lrs*) is described as passing down between the rubro-spinal and lateral cerebro-spinal tracts. It is a tract of small size. These tracts are also called bulbospinal. On the surface of the cord just lateral to the ventral root filaments is the small descending **spino-olivary tract** (Helweg) in the upper cervical region, probably a continuation of the tecto-olivary tract.

Summary of fiber tracts in the cord

The dorsal white column contains:
  Fasciculus gracilis; sensory fibers of lumbosacral nerves.
  Fasciculus cuneatus; sensory root fibers of cervical nerves.
  Lissauer's tract; lateral fine root fibers of sensory nerves.
  Dorsal fasciculus proprius.
The lateral white column contains:
  Dorsal and ventral spino-cerebellar tracts; deep sensibility.
  Lateral cerebro-spinal tract; volitional from motor area.
  Rubro-spinal tract from red nucleus; motor from cerebellum.
  Lateral spino-thalamic tract; sensory impulses to thalamus.
  Lateral fasciculus proprius; for spinal reflexes.
The ventral white column contains:
  Direct vestibulo-spinal tract from Deiters' nucleus.
  Crossed vestibulo-spinal tract from Schwalbe's nucleus.
  Tecto-spinal tract; an optic reflex tract from the tectum.
  Reticulo-spinal tracts from reticular nuclei of stem.
  Ventral spino-thalamic tract; sensory impulses to the thalamus.
  Ventral fasciculus proprius; chiefly crossed spinal reflexes.
  Ventral cerebro-spinal tract; volitional from motor area.

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CHAPTER 18

The Sympathetic Nervous System

The sympathetic nervous system is the name given to the visceral branches of the cranial and spinal nerves, with the exception of the vagus and glossopharyngeal. Everywhere these branches are distributed to smooth muscles of the viscera, to the glands, to the muscular coat of the blood vessels or to the heart. Sympathetic fibers are functionally classified according to the structures they supply: thus there are (*a*) vasomotor fibers to blood vessels, (*b*) visceromotor fibers to muscles of ducts and hollow viscera and (*c*) glandular or secretory fibers to glands. The sympathetic system is by no means an autonomous or independent one. Everywhere it is functionally connected with the spinal cord or brain-stem, through which its reflex arcs are mediated and through which its motor functions may be excited by diverse peripheral, cerebral or sub-cortical connections. Just as in the case of somatic reflexes, the sympathetic system depends on a reflex arc linkage of an afferent neurone, a spinal center, and efferent neurones (fig. 118). There is one difference, the efferent sympathetic neurones are two in number, called by Langley preganglionic and postganglionic. The preganglionic or spinal are the neurones of the first order whose fibers arise from the cells in the sympathetic nucleus (*lh*) of the spinal cord and pass out in the ventral spinal root and visceral branch (white ramus communicans) to end on cells in a sympathetic ganglion. The postganglionic are neurones of the second order whose fibers arise from cells in the sympathetic ganglion and pass back into the somatic nerves as the gray communicating rami or to the viscera as the splanchnic nerves ending either directly in smooth muscle and glands or on cells of the visceral plexuses. In the latter case possibly three neurones exist in the efferent limb of the sympathetic reflex arc, and its functions are inhibitory.

The sympathetic nucleus of the spinal cord (fig. 118, *lh*) forms the lateral horn in the thoracic cord. It is a long discontinuous column of cells about the size and length of a small knitting needle. Its position close to the lateral reticular formation of the cord puts it in close relation to the cutaneous and visceral conduction paths in the lateral fasciculus proprius, cerebro-spinal and reticulo-spinal tracts in the lateral white column of the cord. In the lower lumbar and sacral regions Jacobsohn has identified several other small sympathetic nuclei scattered through the ventral horn. In the thoracic region the fibers of these cells pass out through the ventral root. In the lumbar and thoracic regions many pass out also through

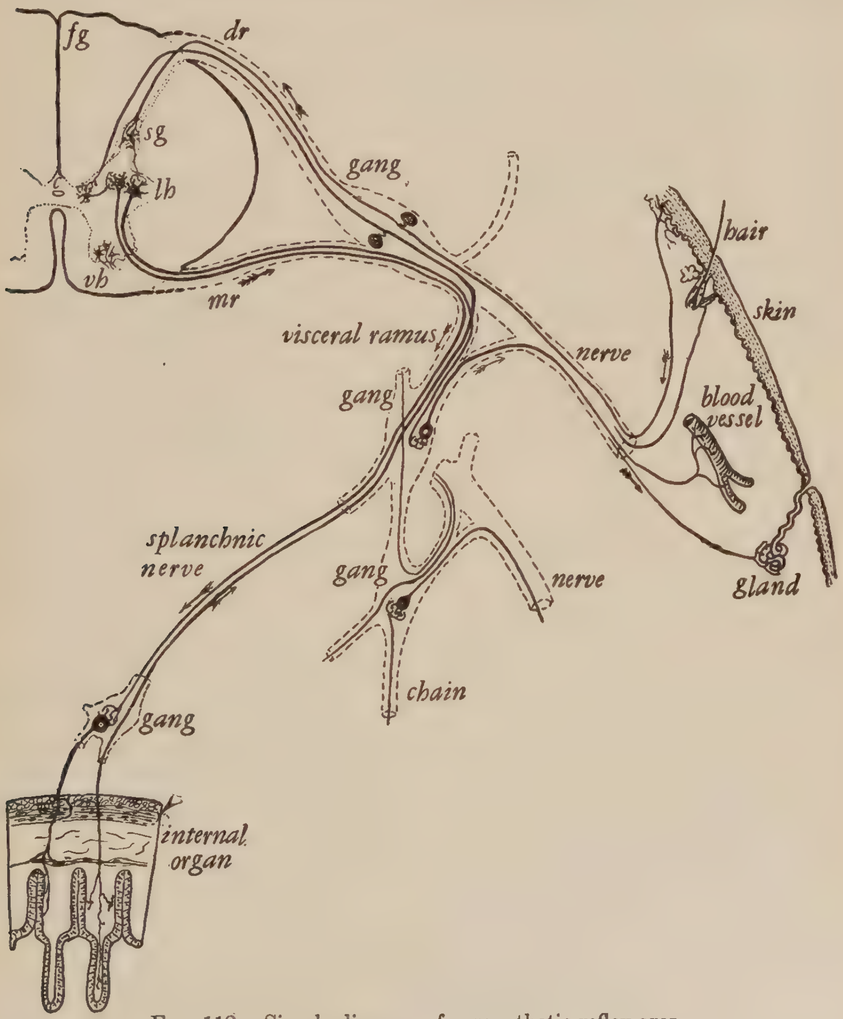

FIG. 118. Simple diagram of sympathetic reflex arcs.

the dorsal root. In both cases they pass through the visceral (white communicating rami) to the sympathetic ganglion, where they end on cells in complicated terminals (figs. 120*A* and 121). There are no sympathetic nuclei or visceral branches in the cervical and lower lumbar regions.

Two general divisions of the sympathetic nervous system are recognized: (1) the somatic division to the sweat glands, blood vessels and erector pilorum muscles of the skin and blood vessels of the striated muscles, of the body wall and limbs; (2) the visceral or splanchnic divisions which supply the smooth muscles, glands and vessels of the viscera (fig. 118).

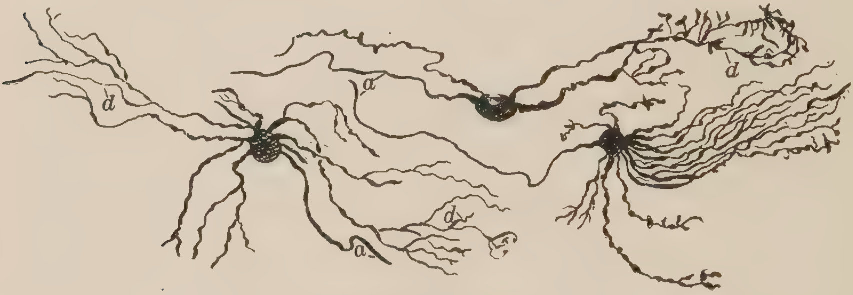

FIG. 119. Neurones of the sympathetic ganglia of a dog. After Cajal.

The somatic sympathetic system

The sympathetic trunk or chain is a long ganglionated cord that runs along the side of the vertebral column from the atlas to the coccyx (fig. 123). Each ganglion is also connected with one or more of the spinal nerves by means of their visceral branches (*rami*). There are three cervical, eleven thoracic, four lumbar and four sacral ganglia in the chain of each side. They vary both in number and size. The white visceral branches of the upper five thoracic nerves enter and end in the upper thoracic ganglia but many stream upward through the ganglia to form the sympathetic trunk of the neck and end in its three ganglia. The white visceral branches of the lower thoracic and upper three lumbar nerves enter and end in the lower thoracic and lumbar ganglia, but many stream downwards through the ganglia to form the lower lumbar and sacral trunk and end in its ganglia. The cells of the ganglia of the entire chain contribute nonmyelinated fibers to the spinal nerves. These form the gray communicating rami. In the peripheral nerves these fibers are distributed to the sweat glands, blood vessels and the erector pilorum muscles of the skin as well as to the muscular coats of the blood vessels of the striated muscles. Many fur covered animals such as the Carnivora have sweat glands only on their palms, soles and tip of the nose. Others, such as most of the Primates and Ungulates, have sweat glands over the entire body. In many animals the erector muscles are well developed and they can bristle up their fur, as for instance, the cat and porcupine. In the human this function appears in the form of "goose pimples." In the furless Primates the vasomotor function of the skin becomes highly developed for (heat regulation) watershifting and perspiration in connection with the conservation or dissipation of heat.

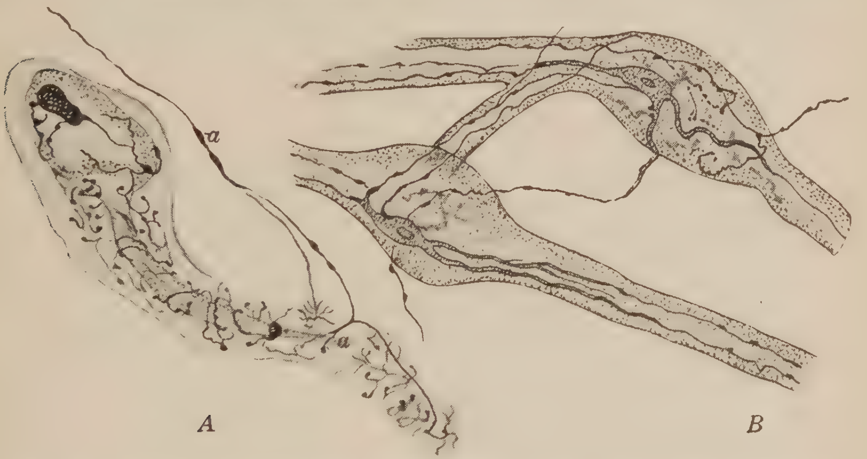

FIG. 120. Neurones from the sympathetic ganglia of (*A*) reptile (after Huber) and (*B*) a rabbit (after Cajal).

From the preceding description it will be seen that the upper five thoracic segments furnish the sympathetic supply for the upper thorax, upper extremities, neck and head; though the vasodilator and secretory fibers for the face pass out in the cranial nerves. The lower thoracic and upper lumbar segments furnish the sympathetic supply for the lower thorax and lower extremities.

The afferent or sensory fibers for these systems of reflex arcs are the heat and cold nerves of the skin and sensory nerves of the muscles. Heat and cold nerves respond to both external and internal heat changes; through the cord and the sympathetic chain ganglia they affect the reflex responses of vascular dilation and sweating of the skin in response to overheating; or vasoconstriction and drying of the skin in response to cold. The afferent fibers probably end in the substantia gelatinosa (fig. 118, *sg*) from which fibers enter the lateral fasciculus proprius, ascend in the cord and make connections with the sympathetic nucleus of the cord (*lh*) by means of collaterals.

The **neurones of the sympathetic nucleus** of the spinal cord (*lh*) are cells of medium size with several widely branching dendrites (figs. 107–109). Collaterals from the lateral fasciculus proprius enter into synaptic relations with these cells and their dendrites, thus completing the spinal reflex arcs. It is also stated that long fibers from higher visceral centers in the brain-stem (reticular nuclei?) descend and end on the sympathetic cells of the cord. The axones of these cord cells form the preganglionic myelinated fibers. They pass out in the ventral root (*mr*) of the spinal nerves; in the lumbar and sacral region also by way of the dorsal root. They then pass through the visceral branch to end in one of the ganglia of the sympathetic chain by means of free endings among the cells, by means of dense entanglements in the glomeruli (*gl*) or by means of dense pericellular entanglements and terminal buttons on the cell bodies (figs. 120, 121).

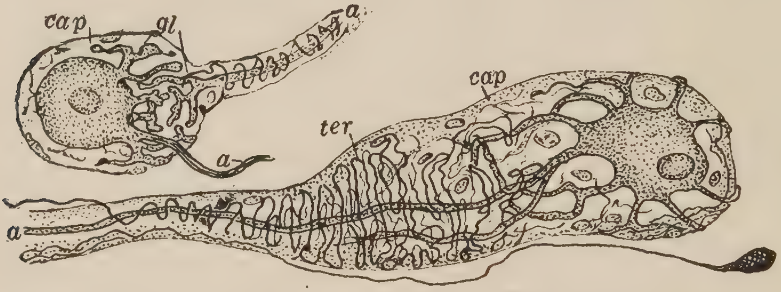

FIG. 121. Neurones from the sympathetic ganglia of man. After Cajal.

Neurones of the sympathetic ganglia (figs. 119–121) have more or less rounded or oval cell bodies. They are multipolar, having several branching dendrites (*d*). These branch out in three ways, (1) long free branches ending among other cells (fig. 119), (2) branches which end in entanglements called glomeruli (fig. 121) in which they form synaptic relations with other neurones, and (3) dendritic clusters which interlace with similar clusters of other neighboring cells.

In man the sympathetic cells are more highly specialized (fig. 121). Many are encapsulated. The cell body is round or oval and sends into the capsule a corona of dendrites, some fine and branching, others short, large and bulbous, and still others pass beyond the capsule and corona to end in nearby glomeruli. By this latter type several cells may be joined into functional groups. Generally the corona is one sided, and is entered by a preganglionic fiber which branches within it. Then, too, the afferent axone may enter and form a spiral entanglement around the axone and throughout the dendritic corona. In the human the individual cells and their synaptic coronas are more isolated than in the lower forms. The axones of these cells form the postganglionic fibers or gray rami of the spinal nerves. They arise from the cell body, or from the base of one of the larger dendrites, describe an irregular course and enter the fiber stratum of the ganglion to pass out in the gray ramus into the spinal nerve. They may pass up or down in the sympathetic chain for some distance before they enter the gray ramus.

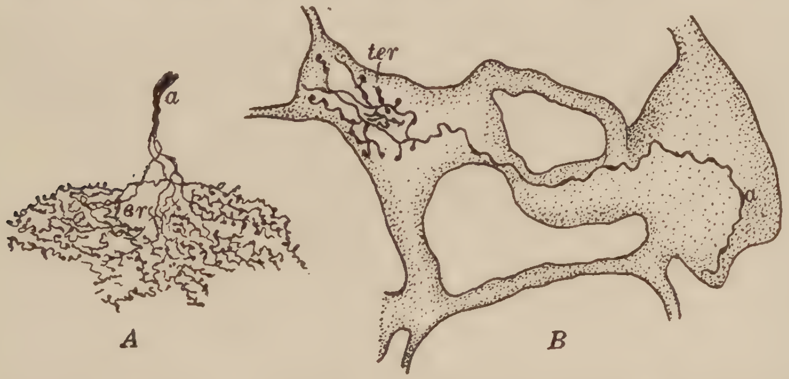

FIG. 122. Sensory endings in viscera (*A*) in endocardium of cat (after Smirnow) and (*B*) at division point of a small bionchus in the lung of a rabbit (Larsell).

The visceral sympathetic system

The visceral sympathetic system includes the splanchnic ganglia and plexuses that are distributed to the thoracic, abdominal and pelvic viscera. The arrangement of neurones follows the plan of the somatic sympathetic system except that the visceral branches are much longer and the ganglia are located near or within the viscera. The visceral afferent fibers arise from cells in the spinal ganglia, pass by way of the visceral branches and plexuses to reach the viscera in which they end in various types of sensory nerve endings (fig. 122, *ter*). The root fibers of these neurones enter the spinal cord in the dorsal root. Their intraspinal connections are not well known (fig. 118), but they are said to end on cells in the region of the central gray. These cells are supposed to enter into synaptic relations with the cells of the sympathetic nucleus of the cord (*lh*). In the lumbosacral region there are several sympathetic nuclei in the ventral horn and their axones pass out by both the ventral and dorsal roots. They pass through the visceral branches, through or by the ganglia of the chain with which as a rule they make no synaptic connection. With the visceral afferent fibers they make up the long splanchnic nerves that reach the viscera in the following groups:

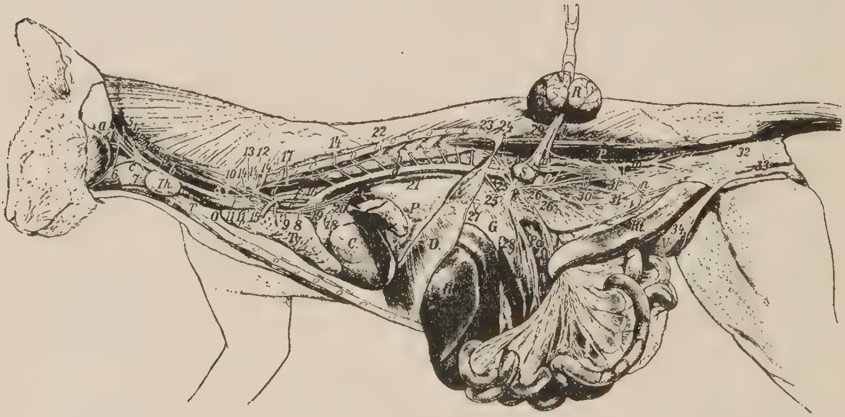

FIG. 123. Dissection of the sympathetic nervous system of a cat. From Ellenbergen and Baum.

The **cardiac nerves** arise from the cervical sympathetic chain and end in the heart and accelerate its action.

The **pulmonary nerves** arise from the upper thoracic nerves and enter the bronchial plexus and end in sympathetic ganglia which in turn supply the smooth muscles and glands in the bronchi.

The **splanchnic nerves** (fig. 123) arise from the fifth to the eleventh thoracic nerves. They pass down beneath the crura of the diaphragm and end in the great celiac ganglia. From the cells of these ganglia arise postganglionic fibers that form the hepatic, gastric, splenic, pancreatic, intestinal, renal and suprarenal plexuses. A part of each plexus supplies the appropriate blood vessels. These plexuses supply the muscular walls of the ducts and of the hollow viscera and the glands of their mucosa. They may end on cells of the myenteric and submucous plexus forming a three neurone system, and exercise an inhibitory influence on the functions of the viscera. The fibers of the **vagus** end directly on the cells of the myenteric and submucous plexuses, forming a two neurone system, and exercise an excitor influence on the motor and secretory functions of these viscera. The hepatic and pancreatic plexuses supply not only the ducts but also the cells of these organs. In the suprarenal glands they supply chiefly the medulla.

The **hypogastric nerves** (fig. 123) arise as visceral branches from the upper two or three lumbar nerves. They supply the descending and pelvic colon and upper part of the bladder through the hypogastric ganglia and plexus.

The **visceral sacral nerves** (fig. 123) arise from the second, third and fourth sacral nerves and enter the various ganglia that form the pelvic plexus. The postganglionic fibers from this plexus supply the rectum, bladder, prostate, seminal vesicles, smooth sphincter of the bladder, cavernous tissue of the penis, tubes, uterus and the walls of all the blood vessels of these organs.

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CHAPTER 19

INTERNAL STRUCTURE OF THE LOWER OBLONGATA THROUGH THE CROSSING OF THE CEREBRO-SPINAL TRACTS

THE medulla oblongata or bulb is the segment of the brain-stem comprised between the spinal cord and the pontal protuberance. Its external features are described in Chapter 12; letters on page xxi.

Sections through the lower oblongata should be studied. When a Weigert series of sections through this level of the oblongata is examined the close resemblance of their internal structure to that of the cord is apparent (figs. 124, 125). The white matter is stained intensely black or blue. It surrounds the *H*-shaped gray matter which appears pale or golden yellow. A deep ventral fissure and a narrow dorsal septum are seen to separate the two halves. In the center is the central canal (*c*).

The **fasciculus gracilis** (*fg*) is seen as a small oval column on each side of the dorsal septum and scattered through its center is appearing an irregular mass of cells, the **nucleus gracilis** (*ng*). When followed up through several sections the nucleus is seen to enlarge and its deep border is seen to unite with gray matter dorsolateral to the region of the central canal. It is apparent that this nucleus has been budded off from the parent gray matter that forms the base of the dorsal gray column comparable to the dorsal nucleus of the cord (*dn*). It must be kept in mind that the fibers that constitute the fasciculus gracilis are a part of the dorsal lumbosacral nerve roots that are prolonged upwards to end in the nucleus gracilis. This has been proven by cutting the dorsal nerve roots or cauda equina which always causes a degeneration of the fasciculus for its entire extent. The fine collaterals seen in the nucleus indicate that the fasciculus is ending there. Cutting the fasciculus or a destruction of the nucleus gracilis does not produce a loss of cutaneous sensibility but gives symptoms of disturbed movement and sensibility in the hind limb which are explained as due to a failure of kinesthetic sensibility to reach the cerebral cortex. In man the destruction of the fasciculus gracilis produces among other symptoms a loss of position and movement in the lower limb.

The **fasciculus cuneatus** (*fc*) appears as a large wedge-shaped tract of fibers dorsal to the dorsal gray column and its neck, and lateral to the fasciculus gracilis. Note the large **nucleus cuneatus** (*cn*) which juts into its deep surface as a ridge-like elevation. It arises from the neck of the dorsal gray column by a broad base so that laterally it is related to the substantia gelatinosa (*sg*) that forms the widely expanded dorsal horn and ventromedially to the intermediate nucleus (*in*) and the gray matter around the central canal. A large number of collaterals entering the nucleus cuneatus indicate that the fibers of the fasciculus cuneatus (*fc*) are ending in the nucleus. Followed upwards the nucleus enlarges and the entering collaterals subdivide it into a large number of cell clusters. The fibers of the fasciculus are derived from the dorsal roots of the nerves of the brachial plexus and those of the thoracic and cervical nerves. For the upper extremity they subserve the same function as the gracilis does for the lower extremity. They conduct deep sensibility from the fore limb and trunk muscles and joints into the nucleus cuneatus which further relays it to the cerebral cortex (to the postcentral gyrus). Note the small dorsal commissure (*dc*) over the central canal (*c*).

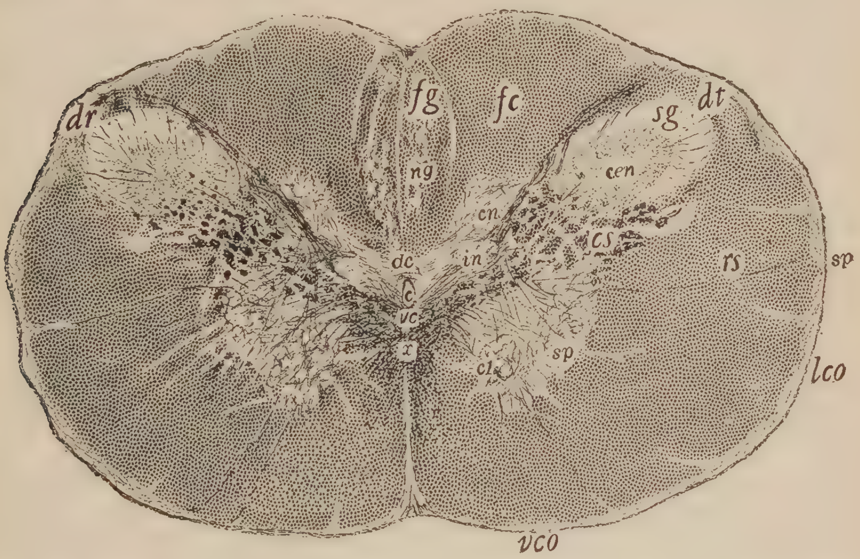

FIG. 124. Section through the lower level of the oblongata of the cat, × 11. Weigert stain.

There is, however, one important difference here; the fibers of the fasciculus cuneatus end not only in the nucleus cuneatus for conduction to the cerebrum but also in the accessory cuneate nucleus (*acn*) situated higher up in the base of the restiform body (fig. 131). This is said to contribute fibers to the cerebellum. That these fibers probably do not excite the cerebellum can be shown by cutting the fasciculus cuneatus and gracilis in an animal in which decerebrate rigidity has been induced. This cutting does not abolish the rigidity whereas cutting the spino-cerebellar tracts (*dsc*) in the lateral column abolishes the rigidity.

The large size of the fasciculus cuneatus (*fc*) is no doubt due to the greater need of the fore limb for a more detailed connection with the cerebrum and cerebellum, on account of the greater complexity and skill of movements required in the fore limb. By cutting the successive cervical nerve roots it has been shown that their fibers have a definite position in the fasciculus cuneatus; the fibers of the first are lateral in the position next to the descending trigeminal root which overlies the substantia gelatinosa. The fibers of the second cervical are medial to those of the first and so on, so that the fibers of the thoracic nerves lie next to the fasciculus gracilis. The cell clusters in the cuneate nucleus in which these root fibers end have a similar relation.

The **descending root of the trigeminus** (*dt*) is a wide crescent of paler staining fibers that covers the surface of the large descending **trigeminal nucleus** (*sg*). Note that it quite encircles the nucleus so that the dorsal tip of the crescent is deeply placed. The many collaterals that stream into the nucleus indicate the termination of the root fibers (*dt*) in it. Followed upward the nucleus and root rapidly enlarge and are displaced laterally by the enlarging cuneate and gracile nuclei. On the surface they form the conspicuous trigeminal tubercle (fig. 128, *dt*).

The trigeminal nucleus (*sg*) is in fact an upward continuation of the gray matter of the spinal cord and has the same structure. It consists of an outer clear zone of fine cells (substantia gelatinosa) in contact with the descending root (*dt*). The root (*dt*) is comparable to Lissauer's tract in the cord. Enclosed within the clear zone is a cellular mass, the central nucleus (*cen*), that stains darkly owing to the fact that it is permeated by a network of fine myelinated fibers. Many collaterals penetrate into this region. Though richly cellular it must be borne in mind its peculiar character depends upon the fine fibers within it, derived in part from the collaterals that end within it and in part from the myelinated axones of the cells of the substantia that pass up to end on cells at higher levels. Cells of larger size occur in its deeper part.

This whole internal system of fibers and cells (*cen*) in the core of the trigeminal nucleus may be looked upon as a manifold cell conduction system, in which the axones are fine and short and cells and synapses are many. In the cord and oblongata it is the only nuclear column that appears to be designed for a simple form of sensory irradiation and preservation of cell activity. This characteristic structure of the trigeminal nucleus extends up in the oblongata to the level of the lower end of the inferior olive (fig. 134) where it is replaced by a compact cellular mass (*nt*) in which the characters of the substantia gelatinosa (*sg*) and central nucleus (*cen*) are no longer recognized, and many small fiber bundles are seen in the region of the latter.

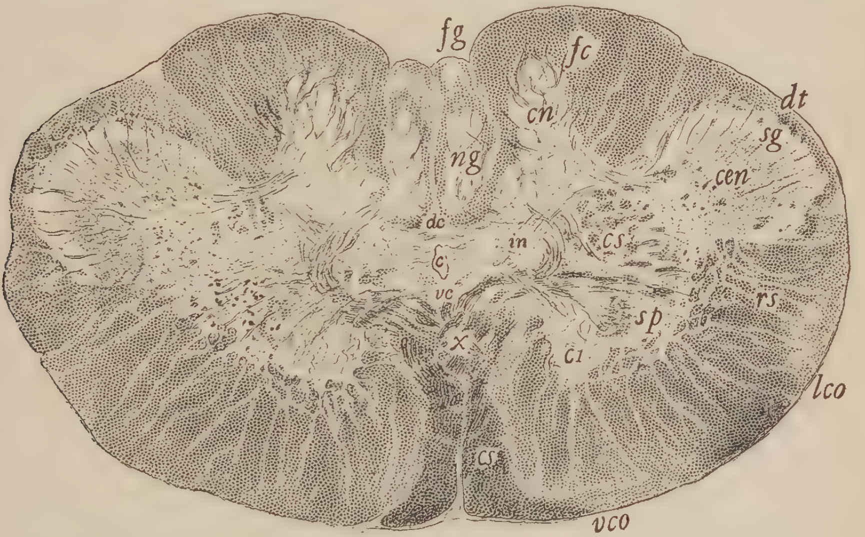

FIG. 125. Section through crossing of the cerebro-spinal tracts of a cat, × 11.

The descending trigeminal nucleus receives through the nerve sensory impressions from the region of the face which is exposed to contacts and to the vicissitudes of heat, cold and painful experiences. When the nucleus is destroyed or when the descending root is cut the animal shows a singular lack of response to cutaneous stimuli such as burning, pinching and pricking of the face. The loss of sensibility proceeds from the neck upwards to the tip of the nose as the lesion proceeds upwards along the descending root.

The lateral and ventral white columns (*lco*, *vco*) consist of many tracts the location of which is the same as shown in figure 114 in the cord, and may be passed by in the present study.

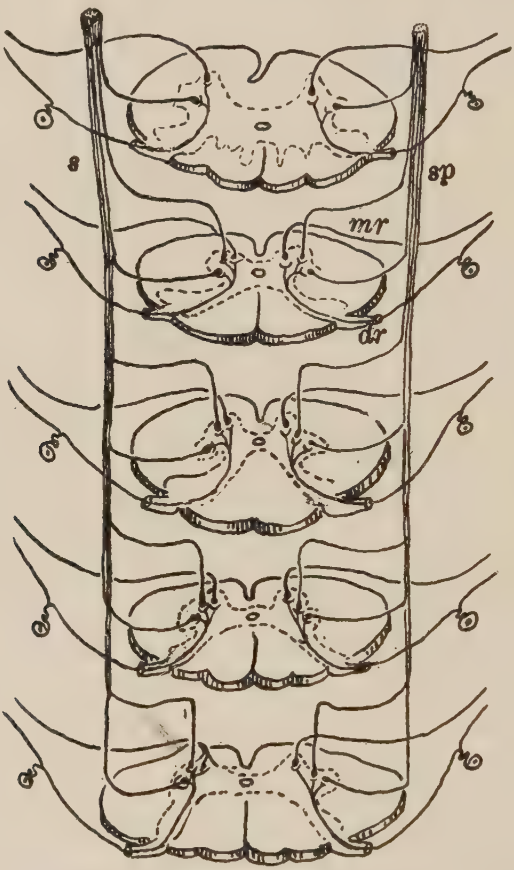

FIG. 126. Diagram of manner of origin of the spinal portions of the spinal-accessory nerve.

The **crossing** (decussation) **of the cerebro-spinal tracts** forms a conspicuous feature of the lower level of the oblongata (fig. 125). These tracts (*cs*) seen on the ventral surface of the oblongata on each side of the median fissure suddenly dip into the fissure and cross through each other ventral to the central canal. They cut through the ventral gray column between the intermediate nucleus (*in*) on each side of the central canal and the nucleus of the first cervical nerve (*c*1) in the ventral horn. Followed down (fig. 124) the crossing (*x*) diminishes in size and the tracts (*cs*) come to form a bundle of fascicles in the neck of the dorsal horn and almost cut the trigeminal nucleus (*sg*, *cen*) away from the rest of the gray matter. At the lower level they enter the lateral white columns (*lco*) and take up a position ventral to the tip of the dorsal horn. Here a spur of gray matter is carried out with them as seen in figure 124. In the Primates and man these tracts are of large size and form prominent round masses ventral to the neck of the dorsal horn which is curved over them.

The cerebro-spinal tracts (*cs*) conduct volitional impulses of cerebral origin to the reflex and motor centers of the spinal cord. Cutting of these tracts frees the reflex and motor centers of the cord from cerebral control producing exaggerated reflexes.

The **ventral horn** or gray column in this region gives origin to: (1) the ventral root of the first cervical nerve (*c*1) which supplies the small suboccipital muscles and (2) the spinal division of the spinal accessory (*sp*) which supplies the sternomastoid and trapezius muscles. Both of these muscle groups are allied with the general musculature of the neck region concerned in movements of the head and of the infrahyoid muscles. As might be expected the nuclei of these nerves represent only the upper end of a general column of cells closely surrounded by the ventral fasciculus proprius (*vp*) of the upper cervical cord which no doubt provides the integrating mechanism for combined movements of these groups. The motor fibers of the first cervical nerve (*c*1) pass out ventrally to form the ventral root. The filaments of the spinal division, however, take a long dorsal ascending course (fig. 126) to finally pass out to the lateral side of the cord where they accumulate to form the spinal portion of the spinal accessory nerve (*sp*). This mode of origin of the nerve is shown in fig. 126. The ascending root fibers (*sp*) occupy a definite position in the lateral side of the ventral gray column ventral to the crossed cerebrospinal tract (figs. 124–125).

The **dorsal root of the first cervical nerve** (fig. 124, *dr*) is seen to enter dorsal to the trigeminal root and nucleus where it forms the most lateral part of the fasciculus cuneatus (*fc*). It is known that this nerve is distributed to muscles of the neck and combines with the hypoglossal to reach the tongue. Its small dorsal root probably conducts deep or muscular sensibility from the occipital region and probably also from the tongue. Over the trigeminal nucleus and crossed cerebro-spinal tract it forms a series of conspicuous curved collaterals that enter the **intermediate nucleus** (*in*) lateral to the central canal. This sytem of fibers is best seen in human sections. According to Cajal who speaks of them as reflexo-motor fibers (fig. 127, *k*) they also end beyond in the motor nuclei of the first cervical and spinal accessory nerves. Close examination of the sections will show that the intermediate nucleus (*in*) sends fibers (*vc*) that cross ventral to the central canal and, perforating the crossing cerebro-spinal tracts, enter the motor nuclei and fasciculus proprius of the other side. These fibers (*vc*) are comparable to the ventral commissure of the cord.

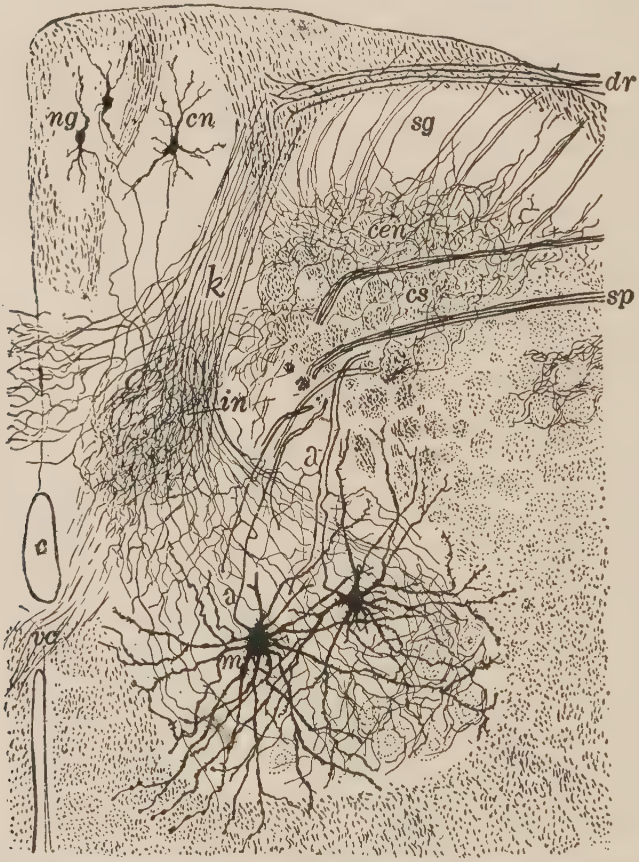

FIG. 127. Section of the oblongata at its lower end, foetal cat, Golgi method. From Cajal.

Another set of collaterals from the dorsal root of the first cervical nerve enters the intermediate nucleus higher up (fig. 129) as it becomes closely associated with the hypoglossal (see page 199). Thus it appears that these connections through the intermediate nuclei provide the appropriate connection for the deep reflexes of suboccipital and tongue muscles.

In a Nissl section taken through this region identify the cells that constitute the substantia gelatinosa (*sg*), the central nucleus (*cen*), the intermediate nucleus (*in*) and the nuclei of the first cervical (*c*1) and spinal accessory nerves (*sp*), the nucleus gracilis (*ng*) and cuneate nucleus (*cn*).

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CHAPTER 20

INTERNAL STRUCTURE OF THE OBLONGATA AT THE OBEX, THROUGH THE HYPOGLOSSAL, VAGAL AND LATERAL NUCLEI

A GLANCE at the dorsal surface of the oblongata (fig. 128) shows that the columns formed by the nucleus gracilis (*ng*) and cuneatus (*cn*) diverge from each other to form a *V*-shaped angle, the **obex.**

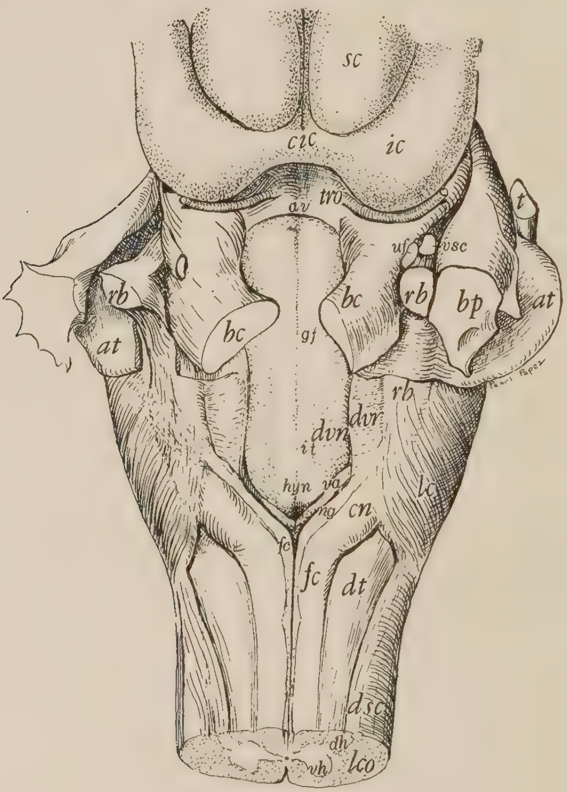

FIG. 128. Dorsal surface of the oblongata of a dog, × 2.

Thus the gray substance over the central canal, known here as the nucleus of the vagus (*va*), becomes exposed to view. To each side it also enlarges and separates to form the two gray wings (alae cinereae) which extend forward in the floor of the fourth ventricle.

At the obex the central canal emerges beneath the commissure formed by the vagal nucleus and widens out to become the fourth ventricle. In the floor of the canal and between the vagal nuclei there appears on each side of the mid-line a slight ridge formed by the **hypoglossal nucleus.**

The **cuneate nucleus** (*cn*) continued forward into the restiform body is here enlarged by a cellular mass within it, the accessory cuneate nucleus (*acn*). Beyond this it is continued into the restiform body (*rb*). The lower external arcuate fibers (*lc*) that join the restiform body (*rb*) by crossing over the surface of the descending trigeminal root (*dt*) arise from the nucleus lateralis which forms a conspicuous projection on the ventro-lateral surface of the oblongata (figs. 73, 74). This should not be mistaken in the lower mammals for the inferior olive. In the Primates the olive is prominent and depresses the nucleus lateralis caudalward and dorsally so that the lower external arcuates appear to cross over the lower end of the olive.

On the ventral surface (figs. 73 and 74) the cerebro-spinal tracts (*cs*) pass on each side of the mid-line and lateral to them the roots of the hypoglossal nerve (*hy*) make their exit. It should be noted that filaments of the accessory part of the spinal accessory (*sp*) make their exit from the lateral side of this part of the oblongata through the dorsal part of the descending trigeminal root (*dt*). The roots of the vagus nerve whose central connections are chiefly in the vagal nuclei (*va*) in the region of the obex enter the oblongata at a higher level.

Sections through the level of the obex should now be examined. Several new features will be seen: the hypoglossal (*hyn*) and vagal nuclei (*va*) appear around the central canal, the gracile and cuneate nuclei give rise to the internal arcuate fibers (*arc*) that turn cephalad to constitute the medial lemniscus (*ml*). In the ventral part the inferior olive makes its appearance and the lateral nucleus (*ln*) interrupts the lateral white column as it ascends in the oblongata. Follow out each of these structures by examining sections below the obex (fig. 129), through the obex (fig. 130), and just above the obex (fig. 131). For the present the inferior olive and medial longitudinal bundle should be identified only; they will be treated more fully in the next chapter.

The (motor) **nucleus of the hypoglossal nerve** (*hyn*) which appears just lateral and ventral to the central canal may be looked upon as an upward continuation of the ventral horn (motor column) of the cord. It lies on the lateral and dorsal border of the medial longitudinal bundle. The medial longitudinal bundle consists of a collection of tracts designated *cvs, ts, mrs* and *vp*. The hypoglossal nucleus may be recognized by its large cells and the succession of root filaments of the hypoglossus nerve which pass out along the lateral side of the medial longitudinal bundle and the cerebro-spinal tract (*cs*). They penetrate the inferior olivary nucleus. Followed upwards the nucleus and root filaments keep this position and end some distance above the obex (fig. 134).

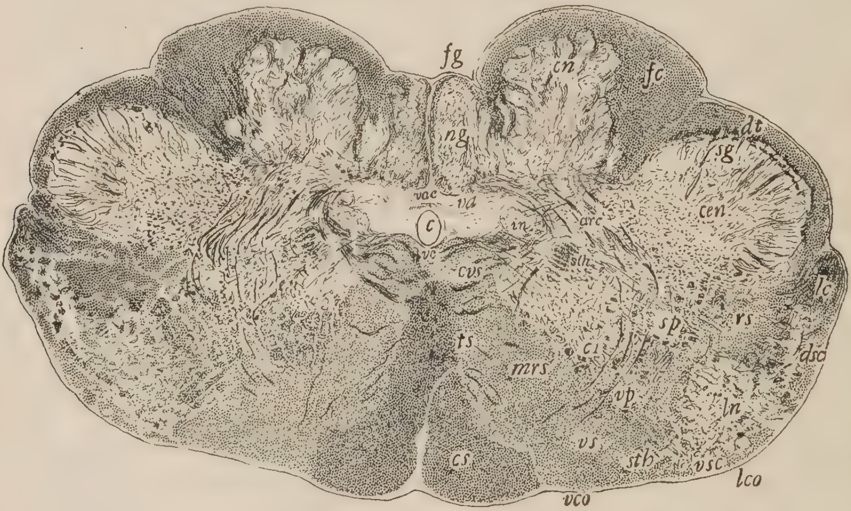

FIG. 129. Section below level of the hypoglossal and vagal nuclei of a cat, × 8½.

The hypoglossal nucleus and nerve are motor, providing the pathway for impulses into the intrinsic muscles of the tongue. On the other hand, it is the lingual nerve that supplies sensory fibers to the mucous membrane of the tongue by which it is able to recognize contacts in the mouth with teeth, lips, cheeks, palate and food. The central root of the lingual nerve and the reflex connections it must make with the hypoglossal nucleus are not definitely known. The same statement may be made in regard to the central connection of the nerves of taste, the chorda tympani and glossal portion of the glossopharyngeal, with the hypoglossal nucleus. It is known that many collaterals pass into the hypoglossal nucleus from the reticular formation lateral to it and these are supposed to constitute some of the reflex connections.

A small **intermediate nucleus** (*in*) is closely associated with the lateral side of the hypoglossal nucleus. At lower levels it is continuous with the intermediate nucleus of the upper cervical region. Like the latter, it receives a reflexo-motor bundle (*k*) from the dorsal roots of the first cervical nerve (descendens hypoglossi). This bundle crosses through the origin of the internal arcuate fibers (*arc*) and reaches the intermediate nucleus of the hypoglossus at its caudal end. It turns in a cephalic direction and passes through the entire length of the intermediate nucleus as fine myelinated fibers which impart to the nucleus its characteristic dark granular appearance. Traced upwards the nucleus comes to lie in the lateral part of the intercalate nucleus (*it*) and its fiber stratum and ventral to the dorsal motor nucleus of the vagus (*mv*) from both of which it must be distinguished. It extends almost to the upper end of the hypoglossal nucleus gradually diminishing and vanishing in the head of the intercalated nucleus. The intermediate nucleus (*in*) is connected with the hypoglossal. Muscle sensibility from the tongue probably reaches it by way of the first cervical nerve and reflexo-motor bundle (*k*). Fibers from the nucleus (*in*) pass to the hypoglossal nuclei of both sides. Note the commissural fibers to which it gives rise (*vc*).

The **intercalated stratum** (*it*) is a layer of fine fibers that caps over the dorsal surface of the hypoglossal nucleus and separates it from the motor vagus nucleus (*mv*) which is a clear mass lateral to it. The fibers in the intercalate stratum are by some authors designated as the dorsal fasciculus of Schutz (*df*). The intermediate nucleus (*in*) is found in the lateral side of this fiber stratum. Both appear to be intimately related to the hypoglossal nucleus into which they send numerous fine collaterals. At lower levels the stratum (*it*) is devoid of nerve cells. Traced upwards small nerve cells appear in it and at the upper end of the hypoglossal nuclei become more numerous and form the **nucleus intercalatus** (*it*) from which the fiber stratum appears to be derived. Throughout its extent a commissure (*vc*) of fine fibers will be seen uniting the strata across the mid-line beneath the ventricular floor and central canal. The functional significance of the nucleus and stratum is not known.

The **vagal nuclei** or alae cinereae (*va*) appear as a clear cellular area over the dorsal surface of the hypoglossal nucleus and intercalated stratum. Below the obex they are united dorsal to the central canal as the commissural nucleus of the vagus in which a delicate system of commissural fibers (*vac*) is seen. Traced upwards the vagal nuclei (*va*) enlarge, separate at the obex and splay out as the alae cinereae lateral to the hypoglossal nuclei in the floor of the fourth ventricle.

Two vagal nuclei are distinguished, best seen in a Nissl section through this level (fig. 132). The **dorsal motor nucleus of the vagus** (*mv*) consists of cells of medium size situated just dorsal to the intercalate stratum (*it*) and intermediate nucleus (*in*). It sends its fibers out through the descending nucleus and root of the trigeminus and external arcuate fibers to the surface to enter the accessory portion of the spinal accessory nerve and the vagus. This is shown in figure 133. Since these cells have the sympathetic cell structure and since their fibers enter the trunk of the vagus this is regarded as the sympathetic nucleus of the vagus. It (*mv*) probably supplies the inhibitor fibers to the heart (nucleus cardiacus). The location of the secretory nucleus for the stomach is not known but is supposed to be near this level. The salivatory centers are at a higher level.

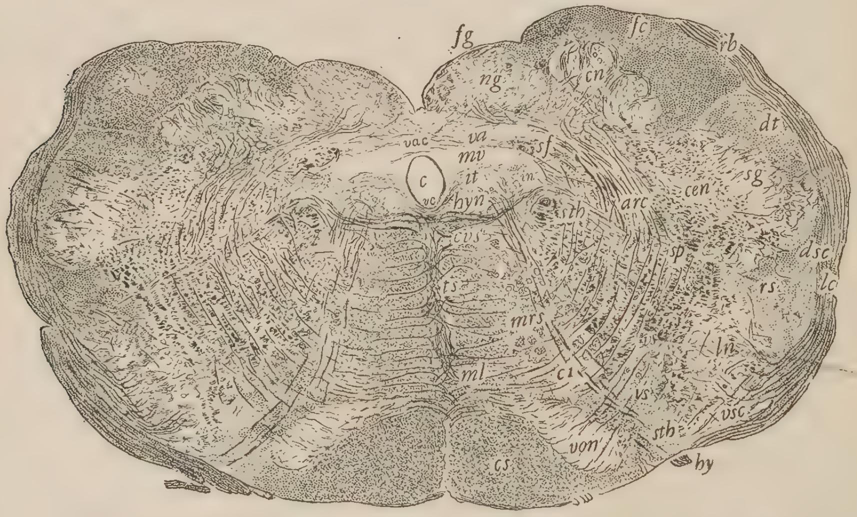

FIG. 130. Section at level of obex through hypoglossal and vagal nuclei, cat, × 8½.

The **sensory vagus nucleus** (*va*) is just dorsal and lateral and closely associated with the foregoing motor nucleus. It appears as a clear area which consists of very fine inconspicuous cells. At the obex and in the floor of the fourth ventricle it is covered in many animals by a raised layer of vascular ependyma. Throughout its length this nucleus stands in intimate relation to the descending

sensory root of the vagus nerve (*sf*) commonly designated the solitary fasciculus. This vagal root always appears as a definite round or oval bundle in the lateral part of the sensory vagus nucleus. Within the sensory nucleus definite cell clusters occur around the root bundle (*va*) and within the bundle. Upwards from the level of the obex the bundle surrounds a small cell mass. At a higher level as the vagus nuclei are beginning to dip under the vestibular (*dvn*) there appear other cell groups. There is one of closely packed cells (*va*) on the dorsolateral side of the root bundle (*sf*) with many fine collaterals passing around and into it. Another smaller group on the lateral side consists of a few large cells (*gu*) surrounded by a dense system of collaterals. At a higher level this lateral mass becomes closely associated with the descending nucleus of the trigeminus (figs. 134 to 136 *gu.*). Here the dorsal motor nucleus (*mv*) comes to lie almost ventral to the bundle and is regarded as a secretory nucleus contributing fibers to the vagus perhaps for gastric secretion and to the glossopharyngeus for salivary secretion. Traced still higher the vagus root bundle (solitary fasciculus, *sf*) is seen to pass out as the root filaments of the two nerves (fig. 136).

In sections above the crossing of the cerebro-spinal tracts the nucleus of the first cervical nerve has disappeared. It is replaced by a diffuse **reticular formation** (*rt*) which consists of numerous longitudinal bundles and curved arcuate fibers (*arc*) scattered through an area of gray matter whose outline vaguely preserves the form of the ventral horn. It appears as if the fasciculus proprius of the cord (*vp*) has here become scattered in the gray matter to form the longitudinal bundles of the reticular formation which surround the ambiguus nucleus (*am*).

In the gray matter of the reticular formation dorsal to the lateral nucleus there appear clusters of scattered cell masses that constitute the **ambiguus nucleus** (*am*). These are an upward continuation of the spinal accessory nucleus (*sp*). From these cells, fibers stream medialwards and obliquely cephalad to the region of the vagus root where they turn lateral and pass out with the other vagus rootlets. Many of them appear to join the root bundle of the vagus (solitary fasciculus) and to pass upward with it making their exit at a higher level. Crossed fibers, some apparently from the intermediate nucleus and others from the reticular formation, are seen to make connections with the ambiguus nucleus. The arched motor fibers derived from the ambiguus nucleus pass out to form the accessory portion of the spinal accessory that joins the vagus to form the pharyngeal plexus. This supplies the pharyngeal constrictors and probably also the œsophageal muscles used in swallowing.

In figure 133 the three sets of root fibers that constitute the vagus group are schematically represented. The sensory fibers that form the descending root or solitary fasciculus (*sf*) arise from cells in the ganglia (*gang*) and end on the sensory nuclei (*va*, *gu*) associated with the descending root. In the case of the intermedius (*i*) and glossopharyngeus (*gn*) nerves such fibers are gustatory, being distributed to the taste buds of the tongue. In case of the vagus (*v*) the sensory fibers are distributed to the pharynx, larynx, bronchial passages, lungs, pericardial region and the stomach. Such sensory fibers are absent in the spinal accessory (*sp*). The motor fibers from the ambiguus nucleus (*am*) are distributed to the pharyngeal muscles, œsophagus and muscles of the larynx. The motor (sympathetic) fibers that arise from the dorsal motor nucleus (*mv*) are distributed to the heart, stomach and salivary glands. For further study see page 221.

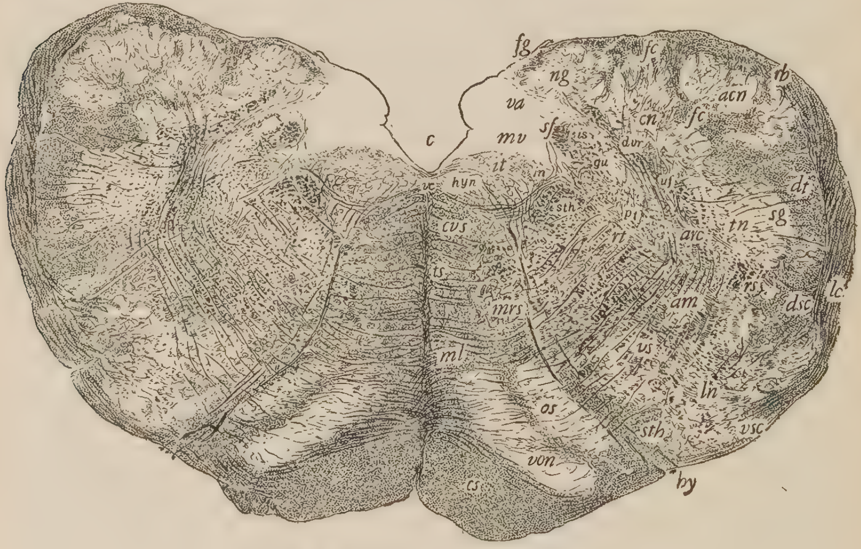

FIG. 131. Section above level of obex, cat, × 8½.

As the **nuclei gracilis** (*ng*) and **cuneatus** (*cn*) are followed upwards (figs. 129, 130) they are seen to increase in size and widen out over the central gray which constitutes the vagal nuclei (*va*). The fasciculi gracilis (*fg*) and cuneatus (*fc*) diminish in size. Above the obex as these columns diverge the nucleus gracilis and its fasciculus end (fig. 131). From the cuneate nucleus proper (*cn*) a large accessory cuneate nucleus (*acn*) is budded off laterally into the caudal end of the restiform body. The cuneate fasciculus (*fc*) ends around this nucleus while from its cephalic surface fibers appear to be contributed to the restiform body (*rb*). From the base or internal surface of the gracile and cuneate nuclei there issues a continuous stream of internal arcuate fibers (*arc*) which arch around the vagus (*va*, *gu*), curve medially and cross the raphe and form a dense stratum of fibers, the medial lemniscus (*ml*) of each side. At lower levels (fig. 129) they form in the midline between the medial longitudinal bundles (*cvs*) which they separate. Here they are so closely applied to the crossing of the cerebro-spinal tracts (*x*) as to

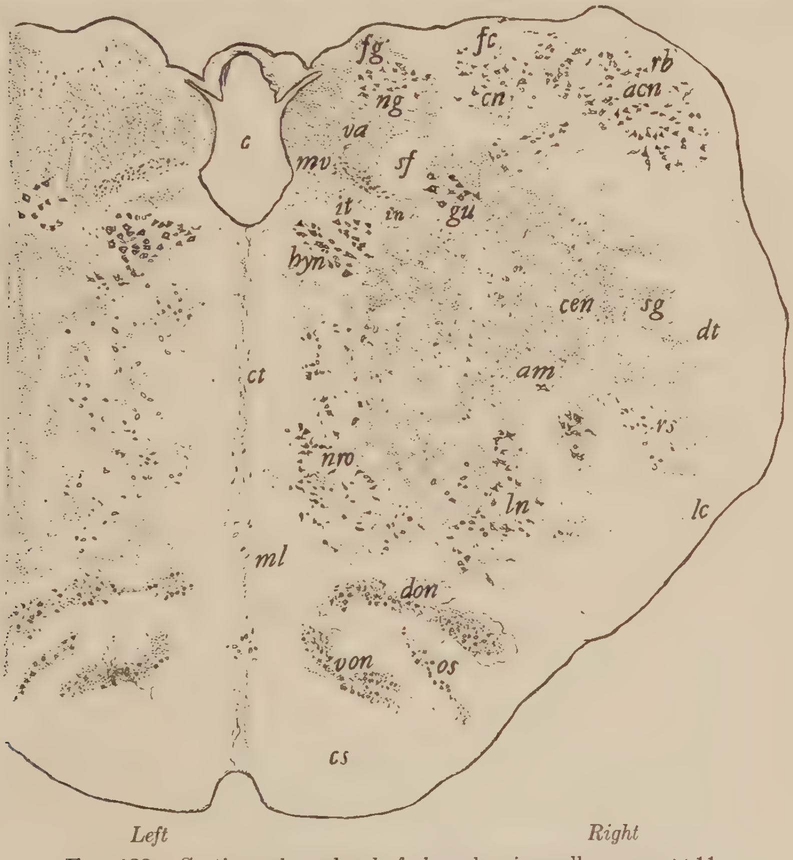

FIG. 132. Sections above level of obex showing cell groups, × 11.

be undistinguishable from it. Traced in sections at a higher level the medial lemniscus (*ml*) forms a definite stratum on each side of the midline between the inferior olives. Here it occupies a position between the medial longitudinal bundle dorsally (*ts*, *mrs*) and the cerebro-spinal tracts (*cs*).

The medial lemniscus (*ml*) continues upwards throughout the brain stem to end in the ventral-lateral or arcuate nucleus of the thalamus (fig. 169, *arc*). It is divisible into gracilo-thalamic fibers and cuneo-thalamic fibers which conduct deep sensibility from the lower and upper limbs and trunk to the thalamus. From the thalamus the thalamocortical radiation (*sr*) delivers these impulses into the sensory area of the coronal or postcentral gyrus. These connections will be studied later.

The **descending root of the trigeminus** (*dt*) and its nucleus (*tn*) in this region (figs. 131 to 134) come to lie ventral to the accessory cuneate nucleus (*acn*), lateral to the reticular formation (*rt*) and are covered on their external surface by the external arcuate or laterocerebellar fibers (*lc*). The clear differentiation between the substantia gelatinosa (*sg*) and the central nucleus (*cen*) is gradually replaced by a more uniform structure of the whole nucleus (*tn*) in which several cell clusters may be recognized. The root is sending in many collaterals which end around the cell clusters. Some of these cell masses are seen invading the root. The small fiber bundles within the nucleus are now becoming more numerous and larger. From the nucleus (*tn*) some fine bundles of arcuate fibers are seen arching medially to enter the medial lemniscus of the other side, on their way to the thalamus.

In the **lateral white column** there appears at this level the large **lateral nucleus** (*ln*) interrupting its course through the oblongata. At many points its internal surface is in connection with the scattered gray matter of the reticular formation. Followed upwards (fig. 134) the lateral nucleus is reduced to a compact mass dorsolateral to the inferior olive (*don*) and some masses scattered near the lateral surface soon disappear. Numerous collaterals are seen to enter the lateral nucleus and many fibers leave its dorsal border to form the external arcuate or laterocerebellar fibers (*lc*). These form a stratum on the outer surface of the trigeminal root and enter the cerebellum as a part of the restiform body (*rb*).

It is known that the spino-thalamic tracts in the ventrolateral column of the cord conduct upwards sensory impulses brought in by the cutaneous spinal nerves (fig. 117). This tract of fibers ends in part in the lateral nucleus. It is therefore supposed that these

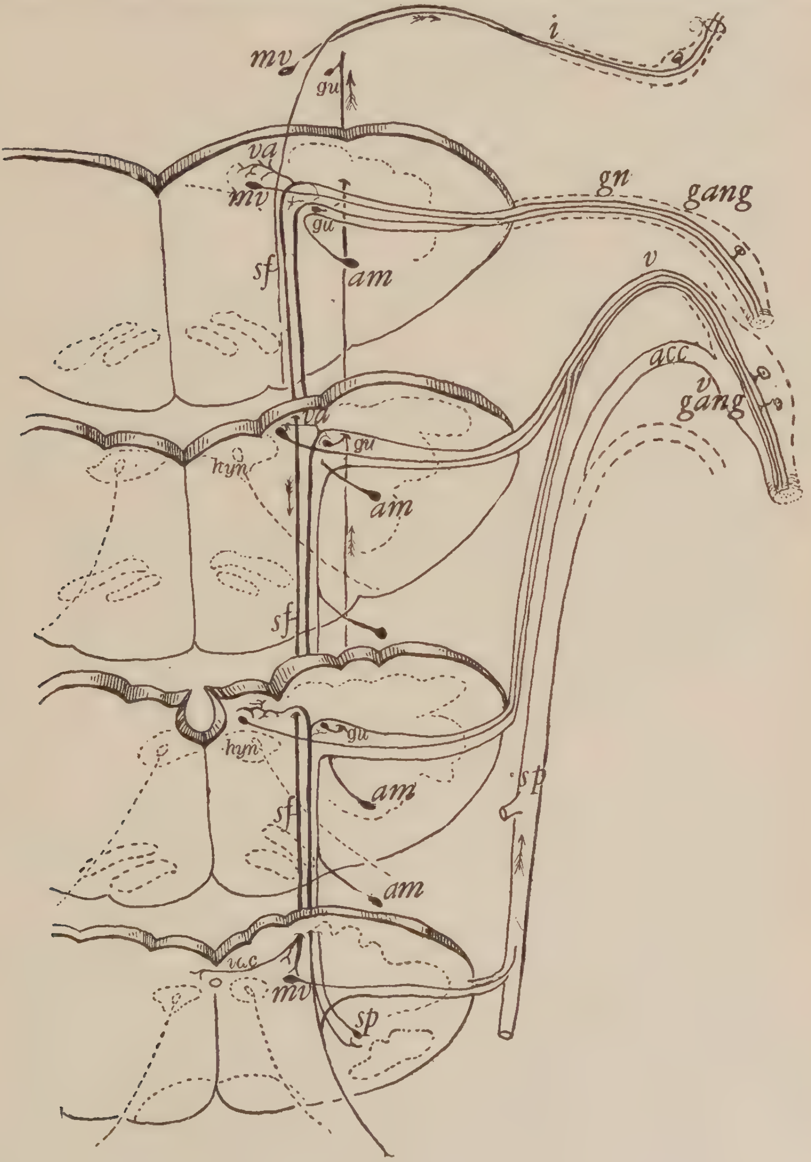

Fig. 133. Schema to show arrangement of vagal nuclei and roots.

impulses, probably of geotropic nature, are distributed to the cerebellum by the laterocerebellar (external arcuate) fibers to induce the appropriate tonic postural response.

The **dorsal spinocerebellar tract** (*dsc*) may be traced over the dorsolateral surface of the lateral nucleus where it joins the laterocerebellar fibers (*lc*) to enter the restiform body (*rb*). The **ventral spinocerebellar tract** (*vsc*) passes upward over the lateral surface of the nucleus to enter the cerebellum in the pontal region. The **rubrospinal tract** (*rs*) forms a dense fiber stratum between the lateral nucleus (*ln*) and the descending trigeminal nucleus (*tn*). In this position it descends into the cord and becomes a part of the lateral column lying just ventral to the crossed cerebrospinal tract.

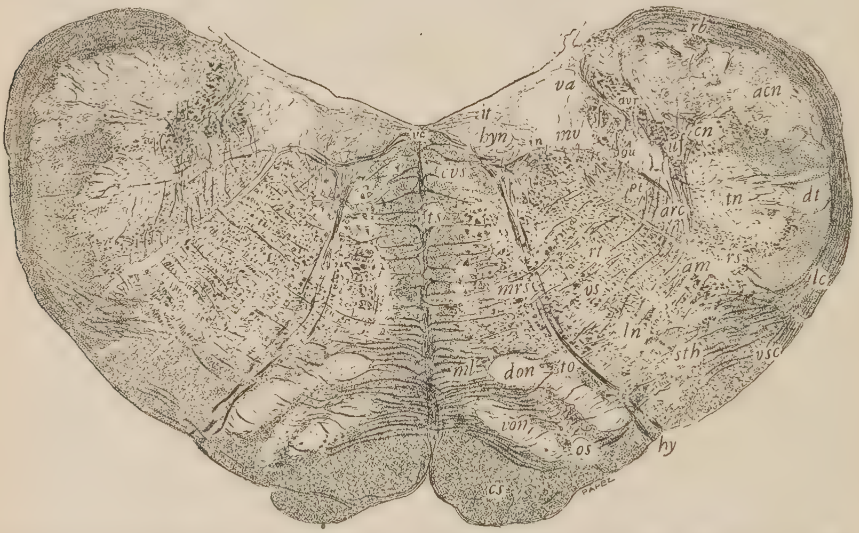

FIG. 134. Section through upper level of the vagal and hypoglossal nuclei, cat, × 8½.

The **direct vestibulospinal tract** (*vs*) forms a dense fiber tract on the medial side of the lateral nucleus and descends in the ventral column of the cord.

A useful demonstration of these fiber tracts is made by cutting the lateral side of the oblongata in a living animal, allowing sufficient time (11 days) for the tracts to degenerate and treating pieces of the oblongata and cord with dichromate and osmic acid. Such sections show that the rubrospinal (*rs*) and direct vestibulospinal (*vs*) tracts degenerate downwards through the spinal cord, while other fibers of the lateral column of the cord degenerate upwards to end in the lateral nucleus. The so-called spinothalamic tracts therefore appear to be interrupted in the lateral nucleus and adjoining reticular formation. It has also been shown that such a cut tends to abolish cutaneous sensibility below the level of the lesion.

In a decerebrate animal it also abolishes decerebrate rigidity on the same side, due to the severance of the spinocerebellar tracts.

At this time review the changing relations of the medial longitudinal bundle (*cvs*, *ts*, *mrs*), cerebrospinal tracts (*cs*) and medial lemniscus (*ml*). At the obex and above (fig. 131) all these tracts form a dense continuous fiber stratum on each side of the midline; the medial lemniscus (*ml*) being between the inferior olives, the medial longitudinal bundle (*ts*, *mrs*) dorsal to it, and the cerebrospinal tract (*cs*) ventral to it on the ventral surface. At the level of the crossing of the cerebrospinal tracts (fig. 129) this crossing (*x*) occupies the midline. The medial longitudinal bundles are on each side of it, and the crossing of the arcuate fibers (*arc*) to form the medial lemniscus is taking place also along the midline just dorsal and close to that of the cerebrospinal tracts. Below the level of the crossing of the cerebrospinal tracts (fig. 124) they come to occupy a position in the lateral column of the cord just ventral to the neck of the dorsal horn and dorsal to the rubrospinal tract (*rs*), while the medial longitudinal bundle has joined the fasciculus proprius (*vp*) to form the medial part of the ventral column of the cord (*vco*).

For identification of the nuclear groups in this region of the oblongata examine a section just above the obex stained by the Nissl method (fig. 132).

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CHAPTER 21

INTERNAL STRUCTURE OF THE OBLONGATA, THROUGH THE RESTIFORM BODY AND INFERIOR OLIVE

STUDY a series of sections through the upper level of the oblongata from the region of the vagal nuclei to the level of the trapezoid body (figs. 135 to 140). The characteristic structures through this region are the restiform body (*rb*), inferior olivary nucleus (*os*, *von*, *don*) and the descending vestibular root (*dvr*) and nucleus (*dvn*). The sensory root filaments of the vagus (*v*) and glossopharyngeus (*gn*) enter at this level to turn down and form the solitary tract (*sf*).

The **restiform body** (*rb*) or inferior cerebellar brachium is a composite fiber bundle which is formed along the dorsal lateral border of the oblongata and enters the cerebellum. It is the chief afferent or sensory connection of the cord and brain-stem with the cerebellum. Through it sensory impulses brought in from the muscles, joints and skin and impulses from the inferior olive and lateral nucleus of the oblongata are conducted into the cerebellar cortex. In this connection the motor function of the cerebellar cortex should be reviewed on page 265. The restiform body is composed of the following fiber tracts (fig. 150):

1. Dorsal spinocerebellar (or Flechsig's) tract.
2. External arcuate or laterocerebellar fibers.
3. Cuneocerebellar fibers from the accessory cuneate nucleus.
4. Olivocerebellar fibers from the inferior olive.
5. Reticulocerebellar fibers from the ventral reticular and arcuate nuclei.

We have seen that the proprioceptive fibers of the dorsal roots of the sacral, lumbar and thoracic nerves are continued upwards to form the fasciculus gracilis. It has been shown that these fibers give off in the cord a linear series of collaterals (fig. 110) which enter the dorsal nucleus (*dn*) and discharge into it, presumably continuously, impulses of deep sensibility from tonic muscles. The dorsal nucleus (fig. 108) extends from the second lumbar segment all the way up the thoracic cord, all along emitting fibers that turn up to form the **dorsal spinocerebellar tract** (*dsc*) on the lateral surface of the cord (fig. 116). The extensive origin of the tract and its long course must be kept in mind. Arriving at the level of the obex (fig. 130) it is seen to turn dorsally with the laterocerebellar fibers (*lc*) constituting the layer of external arcuate fibers which in turn join the restiform body (*rb*) to enter the cerebellum. It has been shown by the degeneration method that this tract enters the median medullary lamina of the cerebellum and through this is distributed to the cortex of the nodulus, uvula and pyramis of the cerebellar vermis chiefly on the same side.

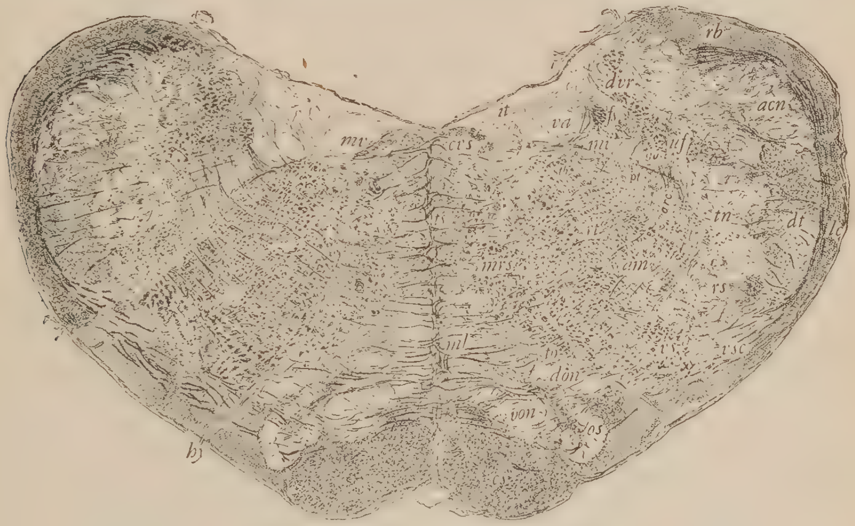

Fig. 135. Section through the middle of the olivary sac, cat, × 8½.

Concerning the origin and spinal connections of the **ventral spinocerebellar tract** (*vsc*) our knowledge is not so explicit. Recent investigations indicate that its fibers may also arise in the dorsal nucleus (*dn*) and probably at higher levels in the cord. They pass upwards in the lateral column of the cord along the ventrolateral surface. The fibers of this are intermingled with the ventral spinothalamic fibers that pass up to end in the lateral nucleus. At the level of the oblongata this tract (*vsc*) of fibers passes over the surface of the lateral nucleus (*ln*) and in the Primates dorsal to the inferior olive. It continues through the oblongata passing over the surface of the facial nucleus (figs. 140 to 146) and superior olive. Here it is closely related to the rubrospinal tract (*rs*) which lies on the ventrolateral surface of the facial nucleus and lateral surface of the superior olive (*so*). Above the superior olive the ventral spinocerebellar tract (*vsc*) passes beneath the brachium pontis and curves dorsally (fig. 72) over the surface of the isthmus and brachium conjunctivum. On the surface of the latter it runs medially to enter the medullary substance of the cerebellum and terminates in the cortex of the anterior lobe (*la*). Thus in origin and ending, it is analogous to the dorsal spinocerebellar tract differing from it in its more ventral position in the cord and its cephalic curved course through the pons and in its termination in the anterior lobe.

It is believed that a continuous discharge of proprioceptive impulses from tonic muscles is delivered into the cerebellar vermis by both of the spinocerebellar tracts. This is indicated by cases of locomotor ataxia and Frederick's ataxia, in which the degeneration affects the fasciculus gracilis, dorsal nucleus and the spinocerebellar tracts, and the reflex tonic condition of the muscles is markedly diminished, and also by the fact that cutting of these tracts abolishes decerebrate rigidity in an experimental animal. In a quiescent decerebrate animal stimulation of the lateral columns induces the rigidity.

We have seen that the lateral column of the cord ends in the **lateral nucleus** (figs. 129–134, *ln*) and that this emits the **laterocerebellar** (*lc*) or external arcuate **fibers** which enter the cerebellum. That this fiber system conducts impulses of cutaneous origin seems likely, but their close association in the cord with the ventral spinocerebellar tract makes such function difficult to show by experiment. It is known that a decerebrate frog retains vestibular tonus, but if the skin is removed from its legs this tonicity is diminished. This suggests that the afferent arc for this tonus is in part of cutaneous origin. The experiments of Magnus have shown that righting reflexes are, in part, of cutaneous origin (see chapter 24).

Study now the formation of the **restiform body** in sections from the level of the obex up to the cerebellum (figs. 129 to 147). At the level of the obex the dorsal spinocerebellar tract (*dsc*) and the laterocerebellar fibers (*lc*) turn dorsally as the external arcuate fibers. These pass over the outer surface of the descending root of the trigeminus (*dt*) to the dorsal surface of the fasciculus cuneatus (*fc*). Here the **accessory cuneate nucleus** (*acn*) is already seen medial to the bundle. Above the level of the obex (fig. 134) the restiform body (*rb*) appears as a definite layer of fibers spread over the accessory cuneate nucleus (*acn*). It is often stated that this accessory cuneate nucleus emits fibers into the restiform body but this is not certain and is not supported by experimental work. Stimulation of the fasciculus cuneatus and gracilis does not affect decerebrate rigidity, which would imply that impulses in these bundles do not reach the cerebellar cortex. The accessory cuneate nucleus gives rise to internal arcuate fibers (*arc*) which enter the medial lemniscus (*ml*) of the other side.

At a higher level (fig. 140) the cuneate nucleus ceases and is replaced by the restiform body. This is now an oval bundle on the lateral side of the combined descending vestibular root (*dvr*) and uncinate bundle (*uf*). Its lower part also overlies the descending trigeminal root (*dt*).

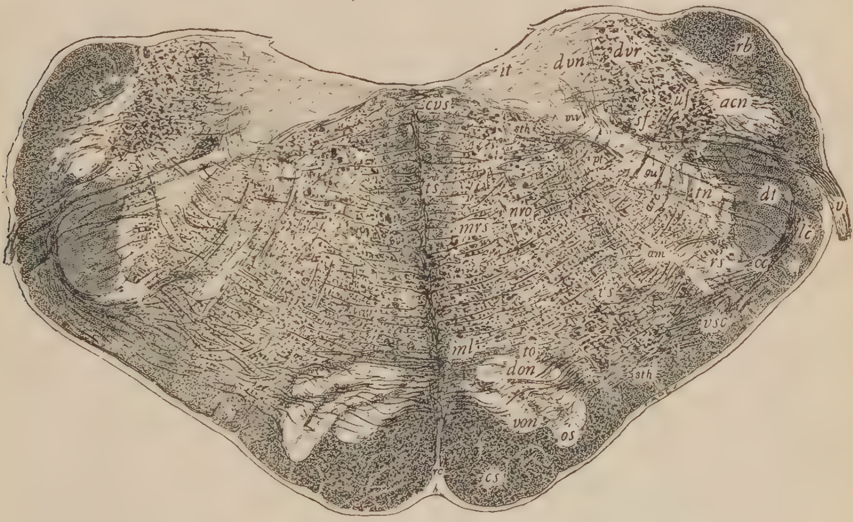

FIG. 136. Section through the upper end of the inferior olive, cat, × 8½

Through the upper levels of the inferior olive the large contingent of **olivocerebellar fibers** (*oc*) is added to the restiform body (fig. 136). These are crossed fibers coming from the inferior olive of the other side. The fibers of the two olives intercross through the midline forming the interolivary crossing (decussation) which passes through the medial lemniscus (*ml*). They penetrate the olive and the lateral reticular formation and stream laterally to join the deep surface of the external arcuate fibers to enter the restiform body. In the Primates in which the olivary sac (*os*) is of great size, very prominent bundles of the olivocerebellar fibers cut dorsally through the trigeminal nucleus (*tn*) and root to reach the inner side of the restiform body.

The **reticulo-cerebellar fibers** (*rc*) or long external arcuate fibers constitute another group added to the restiform body at the upper level of the inferior olive and at the level of the facial nucleus (figs. 140–142). They are inconspicuous in the lower mammals but in the Primates they often form a broad band of fibers that issues from the midventral fissure and sweeps over the external surface of the oblongata to reach the restiform body. Interpolated in their course are seen the **arciform nuclei** either on the medial or ventral surface of the cerebrospinal tract (*cs*). In the lower mammals only a small **nucleus of the raphe** (*nr*) between upper ends of the olives and higher up can be considered as the forerunner of the arcuate nuclei of higher forms. In the Primates in addition to the arcuate nuclei a large nucleus of the raphe occurs in the region of the upper oblongata which also gives rise to the reticulocerebellar fibers. What fibers end on the nucleus of the raphe and on the arcuate nuclei is uncertain; but in man a large band of fibers comes ventrally along the raphe to end on them. This band usually appears to be the most cephalic of the medullary stria of the fourth ventricle which comes down from the region of the superior fovea or locus caeruleus. The acoustic stria (*as*) also plunge ventrally along the raphe before they cross to the other side and the same may be said of other fibers that cross here. The locus is a nucleus on which a small root of the trigeminal nerve ends. This possible connection of the locus with the arcuate cerebellar system would indicate a trigemino-cerebellar connection. It has also been considered that the arcuate nuclei are in reality differentiated out of the ventral reticular nucleus of the oblongata (*vrn*) and like that nucleus receive fibers from the cerebrospinal tracts. If this view is correct they would receive cerebral excitations and relay them into the cerebellum, in which case they may be regarded as an outlying part of the pontal nucleus. The large size of this arcuate system in Primates, in whom the cerebro-pontal connection is very large, favors this view.

The **ventral reticular nucleus** (*nrv*) is a name given to the small cells scattered in the ventral part of the oblongata cephalad to the upper end of the inferior olive between the facial nuclei (figs. 140–143). It is seen best in Nissl sections. These cells appear to receive fibers from the cerebrospinal tracts (*cs*). The cells give rise to the delicate **reticulocerebellar fibers** (*rc*) which pass laterally to enter the restiform body. It is known that some of the fibers cross the midline to become the arcuate cerebellar fibers which enter the restiform body of the other side. Although these fibers are inconspicuous in ordinary Weigert sections of lower mammals they may be seen caudal to the facial nucleus. Any lesion in this region at once produces a

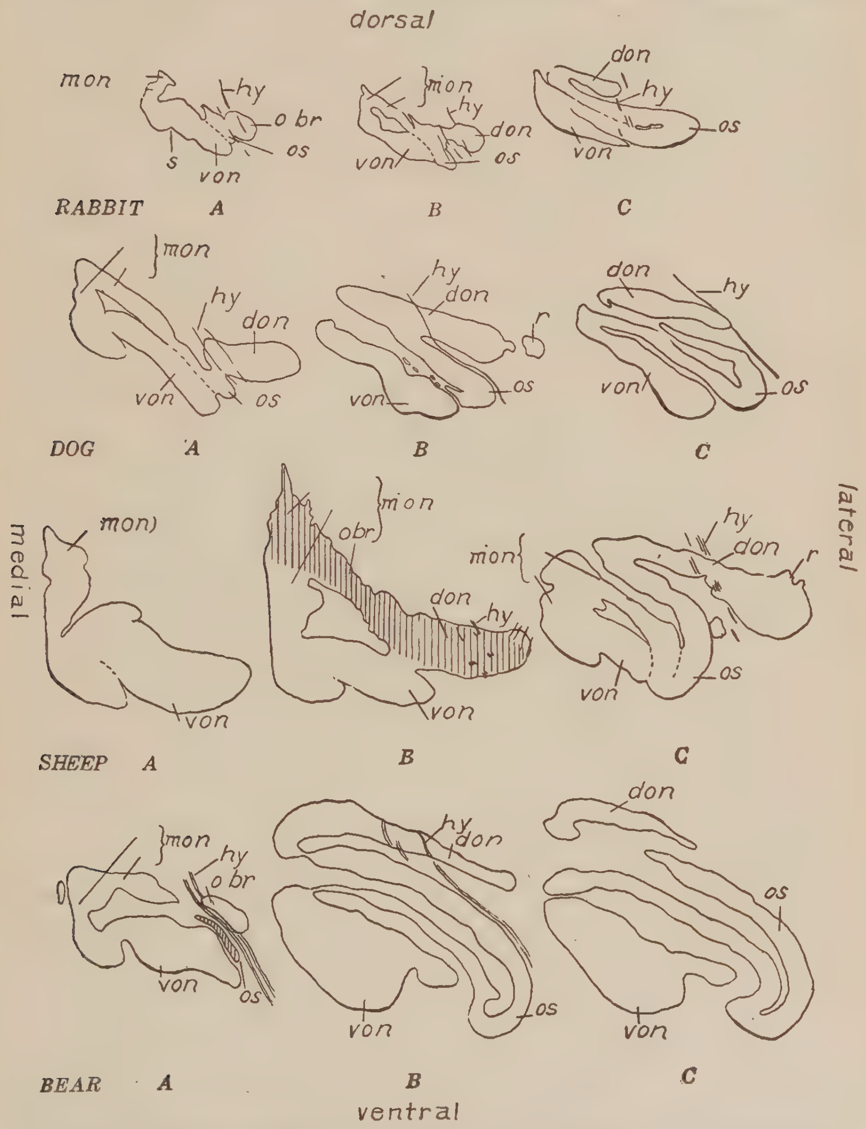

FIG. 137. Sections through the inferior olive of (1) rabbit, (2) dog, (3) sheep and (4) bear. *A* at lower end, *B* and *C* through olivary sac, × 8.

degeneration of such fibers and it has been shown that they end in the floccular lobe. Cases of injury of the lower side of the brachium pontis in man likewise have shown a retrograde degeneration of the cells of the ventral reticular nucleus. Although the long external arcuate fibers are well developed in man the floccular lobe is reduced in size.

It seems likely that the olivocerebellar (*oc*), reticulocerebellar (*rc*) fibers may have functional connections quite different from those of the spino- and latero-cerebellar fibers.

The inferior olivary nuclei

Study now sections that pass through the **inferior olive** and compare with those in figure 137 representing typical sections through this nucleus in the rabbit, dog, sheep and bear. In all mammals the nucleus is divisible into the dorsal (*don*), ventral (*von*) and medial (*mon*) or accessory olivary nuclei and the olivary sac (*os*).

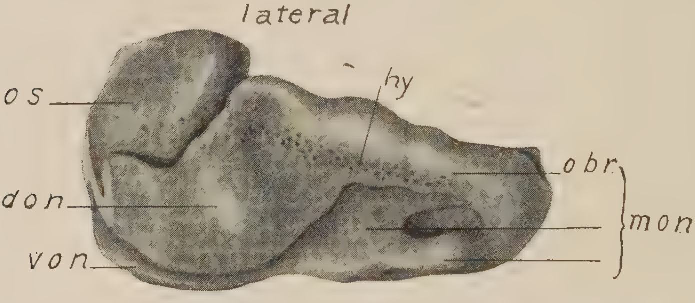

FIG. 138. Dorsal view of model of right inferior olivary nucleus of a rabbit, × 12.

The **olivary sac** (*os*) is a single lamina, folded in the form of a purse with its opening or hilus directed towards the midline. It is seen to best advantage in sections through the upper levels of the olive (fig. 135). It is compressed dorsoventrally so that a dorsal wall and a ventral wall are recognized uniting to form a bottom which projects towards the lateral surface of the oblongata. In its simpler form it is shown in the rabbit (figs. 137, 138). In the dog and cat it becomes larger and in the bear there is a considerable increase in transverse section as well as length of the sac. In the Primates it becomes of great size forming the prominent olivary eminence on the surface of the oblongata ; and its walls present a markedly crumpled appearance. At the hilus the lips of the sac are originally connected by eversion with the dorsal (*don*) and ventral (*von*) olivary nuclei as seen in the rabbit (fig. 137*C*) and sheep. In the higher mammals the sac becomes disconnected from the accessory nuclei by numerous fiber bundles that pass through its medial edge and has a tendency to differentiate as a separate structure. Wax reconstructions of the right inferior olive of a rabbit and dog are shown in figures 138 and 139.

The **dorsal olivary nucleus** (*don*) is an oval plate that lies dorsal to the olivary sac. Its medial border is originally fused with the dorsal lip of the sac from which it separates in the higher mammals in whom the sac is more differentiated. Its caudal end is continued as an oblique bridge (*obr*) to join the medial nucleus (*mon*).

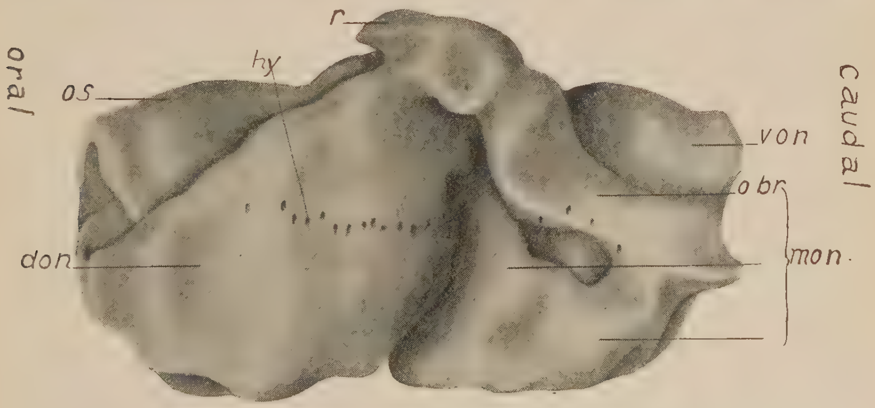

FIG. 139. Dorsal view of model of right inferior olivary nucleus of a dog, × 12.

The **ventral olivary nucleus** (*von*) is an elongated and often much thickened part that extends the entire length of the inferior olive. Its lateral border is free but the bottom of the olivary sac is turned over it and compressed against it in some animals (*e.g.*, Ungulata, fig. 137, sheep). Its medial border is originally fused with the ventral lip of the olivary sac. In Primates on account of the great enlargement of the olivary sac the medial olivary nucleus is displaced over the hilus and is much broken up by the crossing fiber bundles.

At the caudal end of the olive (figs. 137*A*–139) the ventral olivary nucleus and the olivary bridge extend beyond the olivary sac and are united by a median vertical plate, the **medial olivary nucleus** (*mon*). This, in some cases, forms a prominent ridge on the ventral side. It is from the lateral flexion of such a vertical plate (*mon*) that the olivary sac is developed in the upper extent of the olive. The wax models show these relations. The caudal end of the olive may be regarded as a more primitive portion in which the olivary sac has failed to differentiate from the medial olivary nucleus.

The outgoing root filaments of the hypoglossus nerve (*hy*) perforate the dorsal accessory olive and to some extent the sac in most of the lower mammals, but in the Primates, on account of the great enlargement of the sac, these filaments pass through the region of the hilus.

The cells of the olive emit the olivocerebellar axones that cross the midline forming the interolivary crossing (decussation). They enter the restiform body and are distributed to the cortex of the cerebellum. If this crossing is cut in an animal the olivocerebellar fibers degenerate. It has been shown that when the lateral cerebellar lobes fail to develop the olivary sac is also wanting. After injuries or softenings of the lateral lobes corresponding areas of atrophy also occur in the olivary sac. The accessory olivary nuclei are, on the other hand, connected with the cortex of the vermis. In the birds in whom the cerebellum is practically limited to the vermis the olivary sac is wanting and the olive resembles the lower end of the mammalian olive. It seems likely that the functional connections of this lower end are more primitive and differ from those of the larger upper portion that contains the sac. The afferent connections of the inferior olives are not understood (fig. 166). It seems likely that fibers pass up from the fasciculi proprii of the cord and end on cells of the accessory olivary nuclei. Their source is not known. It is known that the olivary sac receives fibers from higher levels (*teg*) that pass down through the central tegmental bundle. They are called the tecto-olivary tract. The origin of this tract is unknown but lies in the region ventral to the superior colliculus. In case the olivary sac fails to develop this tract also fails to develop. In the oblongata this tract accompanies the direct vestibulospinal tract as far down as the olive. The terminals in the olivary sac form complex bush-like arborizations in which the olivary cells and their dendrites are embedded. It seems likely that the inferior olivary sacs are concerned with some phase of the motor functions mediated by the midbrain (tectum), subthalamus and cerebellum.

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CHAPTER 22

Internal Structure of the Upper Oblongata, through the Descending Vestibular and Facial Nuclei

Examine sections through the upper level of the oblongata (figs. 140 to 143). In this study special attention should be given to the descending vestibular root (*dvr*) and nucleus (*dvn*) and the facial nucleus (*fn*) and nerve (*f*). In these sections the inferior olive disappears. The reticular formation is greatly enlarged and contains in it the facial nuclei and special fiber tracts that will be discussed later. In these sections the oblongata has widened out so that the floor of the fourth ventricle is seen as a wide dorsal surface covered by the vestibular nuclei. Figure 150 represents a simplified arrangement of the descending vestibular root and nucleus.

Examine now the large quadrilateral fiber tract (*dvr*) along the medial side of the restiform body (*rb*). Note its distinctive appearance. Its fibers are scattered as small bundles among which some gray matter is dispersed in a manner resembling the reticular formation. This bundle consists of the large **descending root of the vestibular nerve** (*dvr*) and the **uncinate fasciculus** (*uf*). These two sets of fibers are so intermingled that they cannot be distinguished as separate bundles. In a general way the fibers of the uncinate fasciculus (*uf*) occupy a more lateral position and are crowded into the angle between the restiform body and the descending root of the trigeminus (*dt*). The descending root of the vestibular nerve (*dvr*) forms the scattered medial bundles that lie next to the nucleus (*dvn*).

Along its medial side is the long **descending vestibular nucleus** (*dvn*). In cross section it is triangular. It covers the reticular formation and forms the lateral part of the floor of the fourth ventricle partly overlapping the descending root (*dvr*) and is partly invaded by it. Throughout its extent this nucleus receives great quantities of fine collaterals from the descending vestibular root and uncinate bundle. These collaterals are seen permeating the nucleus and imparting to it, in Weigert sections, a dusky appearance. The gray matter dispersed within the root may be regarded as the interstitial part of this nucleus. In the Primates a distinct cell mass derived from the accessory cuneate nucleus occurs within the lower end of the root.

Experimental section of the descending vestibular root (*dvr*) and limb of the uncinate bundle (*uf*) shows that they end exclusively in the descending vestibular nucleus (*dvn*) by means of collaterals. At lower levels (fig. 134) they are seen to pass medial to the accessory cuneate nucleus (*acn*). And many arcuate fibers (*arc*) from the latter penetrate their ventral surface and should not be confused with vestibular arcuate fibers. The descending vestibular root and nucleus rapidly dwindle in size as they near the level of the obex (fig. 131). Here they (*dvr, uf*) are compressed between the cuneate (*cn*) and vagal nuclei (*gu*) and soon end on a level with the upper end of the nucleus gracilis (*ng*).

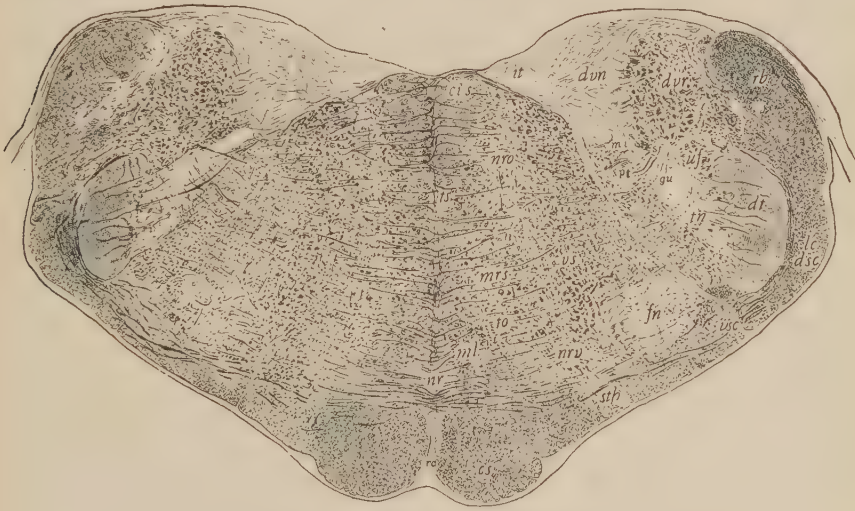

FIG. 140. Section just above the inferior olive, cat, × 8½.

Examine now the ventral surface of the descending vestibular root and nucleus at higher levels (fig. 141, *dvr*, *uf*). This surface is oblique and lies over the reticular formation. Embedded in this surface is the upward prolongation of the vagal nuclei (*mv*) or ala cinerea and the accompanying solitary fasciculus (*sf*) formed by the combined descending sensory roots of the vagus (*v*) and glossopharyngeus (*gn*) and intermedius nerves (*i*).

The descending vestibular nucleus (*dvn*) is seen to emit from the entire extent of its ventral surface a system of **vestibular arcuate**

fibers (*cvs*). These are seen to cut through the vagal nuclei (*mv*) as curved bundles that arch medially through the dorsal part of the reticular formation and cross the midline. Actually they turn down in the dorsal part of the medial longitudinal fasciculus. Here they form the **crossed vestibulospinal tract** (*cvs*), one of the important components of this fasciculus. In this tract they extend down through the whole length of the oblongata and spinal cord. At the level of fig. 135 the vestibular arcuate fibers diminish in number and are replaced by arcuate fibers (*arc*) which enter the medial lemniscus (*ml*). These arcuate fibers coming from the nuclei gracilis and cuneatus occupy a more ventral and lateral position in the reticular formation and are not seen above the level of the inferior olive. The numerous arcuate fibers passing through the reticular formation at the level of the facial nucleus (fig. 141) are derived mostly from the descending and medial vestibular nuclei of the two sides, crossing to descend as the crossed vestibulo-spinal tract (*cvs*). Medial to the descending vestibular nucleus (*dvn*) and connected with it is the nucleus intercalatus (*it*) which looks much like it but is distinguished as a separate nucleus.

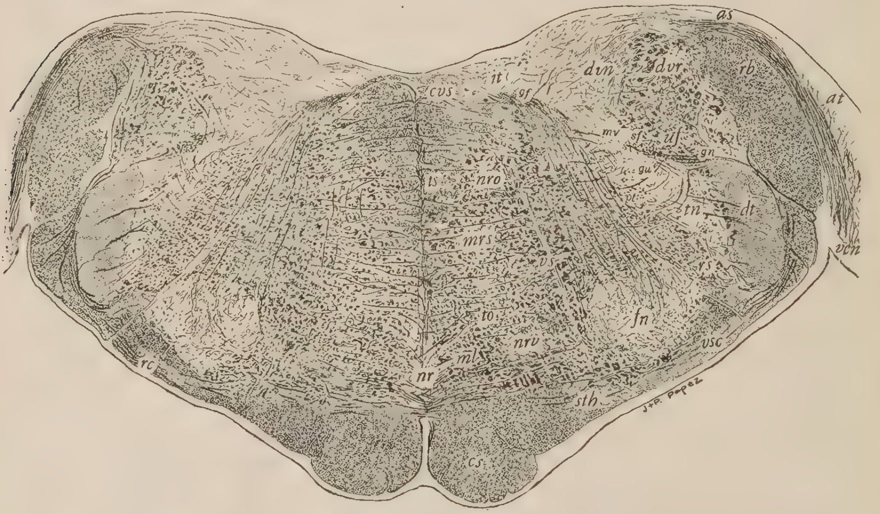

FIG. 141. Section through the level of the facial nucleus and glossopharyngeal root, cat, × 7½.

A theory of function of the descending vestibular nuclei and crossed vestibular tracts may be formulated from their anatomical nature and connections and from experimental evidence. The functions of any center and tract which it emits are dependent upon the source of impulses that are discharged into the center, the nature of its synaptic connections, cell structure and terminal connections of the axones that form the tract. Thus in regard to the functional connections of the descending vestibular nucleus (*dvn*) it should be kept in mind that through the descending root (*dvr*) it receives excitations from the ampullary organs of the vestibule and semicircular canals, and that through the uncinate fasciculus (*uf*) it receives excitations from the fastigial nucleus (*fas*) of the cerebellum. The brush-like collaterals of these fibers ending in the nucleus (*dvn*) are shown in figures 136 to 143: The cells of this nucleus are small and crowded together. Any explanation of the function of this nucleus must take into account these connections and peculiarities. Undercutting or injuring the nucleus on one side causes a degeneration of the crossed vestibulospinal tract (*cvs*) and a hypertonic condition of the limb muscles of the other side. If the injury is severe enough to affect a large part of the fibers the contralateral hypertonia will produce symptoms of rotation to the injured side whenever the animal makes any attempt to move. When both crossed vestibulospinal tracts are cut in the midline of the oblongata a striking bilateral hypertonia of the limbs ensues, which resembles that seen in decerebrate rigidity. There is a marked extension and stiffness of the limbs which resist passive movement. From these results it seems that the crossed vestibulospinal tracts inhibit or decrease extensor tonus of the muscles. As will be shown later the extensor tonus is maintained through the direct vestibulospinal tract (*vs*) that comes from the lateral vestibular nucleus. It is also known that there is a far more extensive cerebral area devoted to extensor (antigravity) functions than to flexor functions. The flexor and extensor functions are reciprocal, and it seems likely that these crossed and direct vestibulospinal tracts participate in this reciprocal arrangement.

The **vagal nuclei** (*va*, *mv*, *gu*) and roots (*sf*) have been studied in chapter 21. They should now be followed out as they are continued upwards and embedded in the deep surface of the descending vestibular nuclei. At this upper level (figs. 140–142) the nuclei belong more to the glossopharyngeus and intermedius nerves. It must be kept in mind that the sensory roots of these three nerves enter in succession at the upper level of the oblongata and turn down to form a single compact root bundle, the solitary fasciculus (*sf*). The nuclear masses associated with the solitary fasciculus also form a continuous column (fig. 133, *va*, *mv*, *gu*, *am*). It is therefore not possible to assign any particular cell group exclusively to any one of these three nerves. In fact the cell groups and central connections made by these nerves are, so far as is known, merged into a common functional column for taste, salivation, hunger, gastric secretion and swallowing, and for cardiac and pulmonary functions. The motor filaments from the dorsal motor nucleus of the vagus (*mv*) as well as the loops from the ambiguus nucleus (*am*) pass out directly ventral to the solitary fasciculus without taking any large part in its formation (fig. 133).

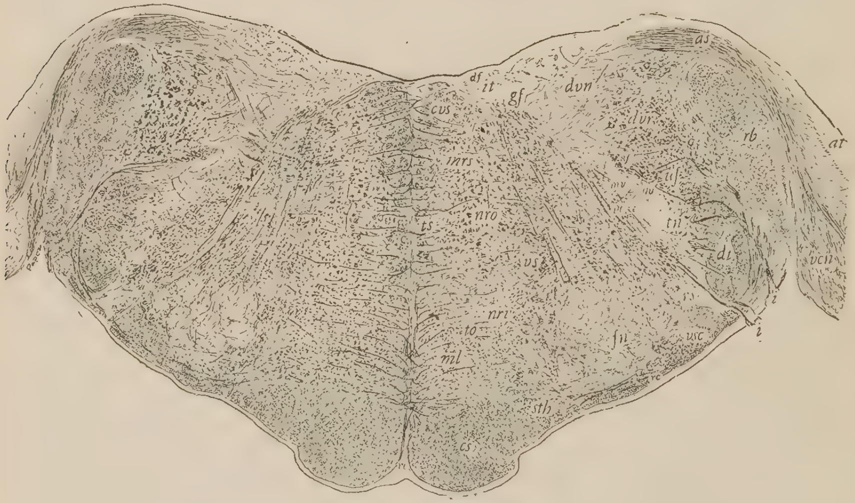

FIG. 142. Section through the level of the cochlear and facial nuclei, cat, × 7.

Begin with a section just above the obex (fig. 134). Note how the sensory vagal nuclei (*va*, *mv*, *gu*) diminish in size and become gradually covered over by the descending vestibular nucleus (fig. 136). At this level they are believed to constitute the gustatory and salivatory nuclei. The gustatory nucleus (fig. 132, *gu*) closely surrounds the solitary fasciculus (*sf*) from which it receives the taste fibers and probably also the sensory gastric fibers. The salivatory nucleus is probably the dorsal motor nucleus of the vagus (*mv*) medial to the solitary fasciculus (*sf*) and emits the secretory fibers that pass to the salivary and probably also to the gastric glands. Many vestibular arcuate fibers cut through these nuclei. At higher levels the sensory nucleus (*va*) disappears but the salivatory nucleus (*mv*) and the gustatory nucleus (*gu*) are continued upwards for a longer distance (figs. 135–143) as the nuclei connected with the glossopharyngeal (*gn*) and intermedius (*i*) nerves.

At this upper level there appears a new mass of cells ventral to the gustatory nucleus (*gu*) and closely associated with the trigeminal nucleus. Of this it is in reality a part, for it receives many collaterals from the dorsal medial part of the descending trigeminal root.

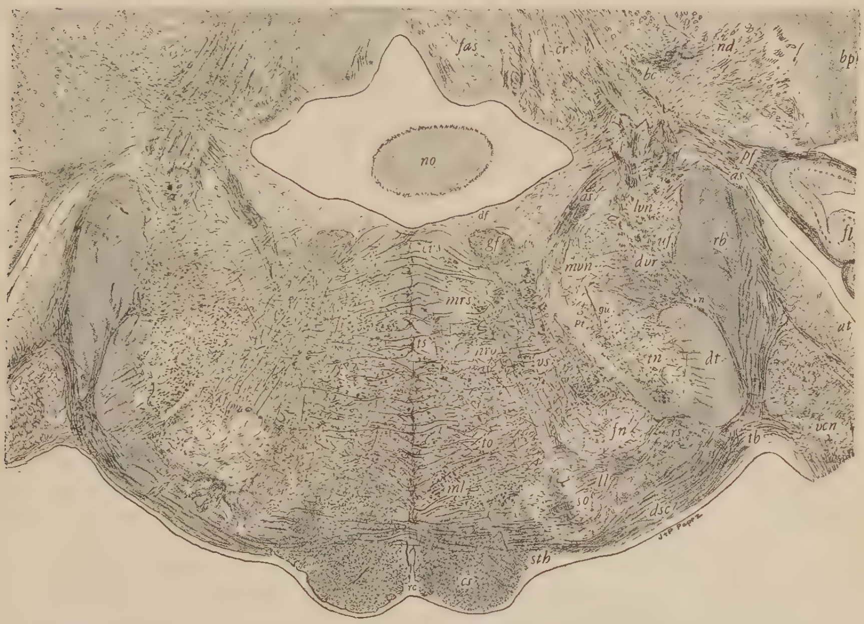

FIG. 143. Section through the level of genu of facial nerve and lateral vestibular nuclei, cat, × 7.

Though such a relation may be made out at lower levels it is most evident at these higher levels. This is the column of cells by some (Yagita) identified as the salivatory nucleus. It should be distinguished from the salivatory nucleus (*mv*) which in this region is an upward continuation of the dorsal motor nucleus of the vagus. But it will be noticed that these nuclei are actually confluent ventral to the solitary fasciculus. Medial to them the fibers of the reticular formation constitute the tract of Probst (*pt*) which is formed by descending branches from the mesencephalic root of the trigeminus. This tract of fibers extends from the region of the mesencephalic root as far down as the obex and is all along closely associated with the nucleus ventral to *gu*. In this connection it should be kept in mind that the buccal, lingual, labial and alveolar branches of the trigeminus are concerned with oral sensibility and insalivation, and a central connection with a special nucleus in this region might be expected.

The root filaments of the vagus, glossopharyngeus and intermedius should be followed out by a close examination of the sections. One can distinguish the motor and sensory filaments of these nerves according to whether they pass through or over the descending trigeminal root and nucleus (fig. 136). All along the delicate filaments that leave the dorsal motor nucleus of the vagus can be traced laterally between the solitary fasciculus (*sf*) and Probst's tract (*pt*) through the descending nucleus and root of the trigeminus to the surface to join the vagus (figs. 133, 136) and glossopharyngeal nerve trunks. Other filaments come from the ambiguus nucleus (fig. 135, *am*) and make dorsomedial loops through the reticular formation. These loops are medial to the dorsal motor nucleus of the vagus (*mv*). On account of their oblique upward course the loops are hard to find in the sections. From these loops the fibers pass out like the others but in a more ventral position. These motor filaments are seen passing out as two or more strands ventral to the sensory filaments that enter the solitary fasciculus. As the solitary fasciculus (*sf*) is followed to higher levels its fibers are seen to pass out in small fascicles dorsal to the trigeminus root to join the sensory parts of the vagus (fig. 136, *v*), glossopharyngeus (fig. 141, *gn*) and intermedius (fig. 142, *i*) nerves. The intermedius nerve enters the surface of the oblongata beneath the cochlear nucleus (fig. 142, *i*) on a level with the middle of the facial nucleus (*fn*). It turns down to form a flat bundle (*sf*) dorsal to the salivatory nucleus (*mv*). Above this level the solitary fasciculus is no longer present, but is replaced by a small root bundle of the trigeminus nerve.

The facial nucleus and nerve

In these sections through the upper end of the oblongata identify the **facial nucleus** (*fn*). It lies in the ventrolateral side of the reticular formation close to the surface. Find the numerous filaments that stream out of its dorsal surface (figs. 141–143). These constitute the first part (pars prima) of the facial nerve. They pass dorsomedially and turn forward (*gf*) under the descending vestibular nucleus. They accumulate into a compact round bundle (*gf*), the genu of the facial nerve. This can be followed upwards for some distance before it curves laterally to pass out as the outgoing limb (pars secunda) of the facial nerve (fig. 147). Note that the facial genu (*gf*) forms an elevation in the floor of the fourth ventricle on each side of the midline. Lateral to the genu is the **medial vestibular nucleus** (*mvn*). Medial to it is the **crossed vestibulospinal tract** (*cvs*). Dorsal to it is a crescent of fine fibers, the dorsal fasciculus (*df*). Ventral to it (fig. 146) is the abducens nucleus (*an*). Many fibers will be seen crossing beneath the genu of the facial nerve (*gf*) to reach the midline. Some of these are the crossed vestibular root (figs. 141–143), some are crossing vestibulo-mesencephalic fibers and others (figs. 146–147) are fibers from the olivary peduncles (*op*) which cross at this point.

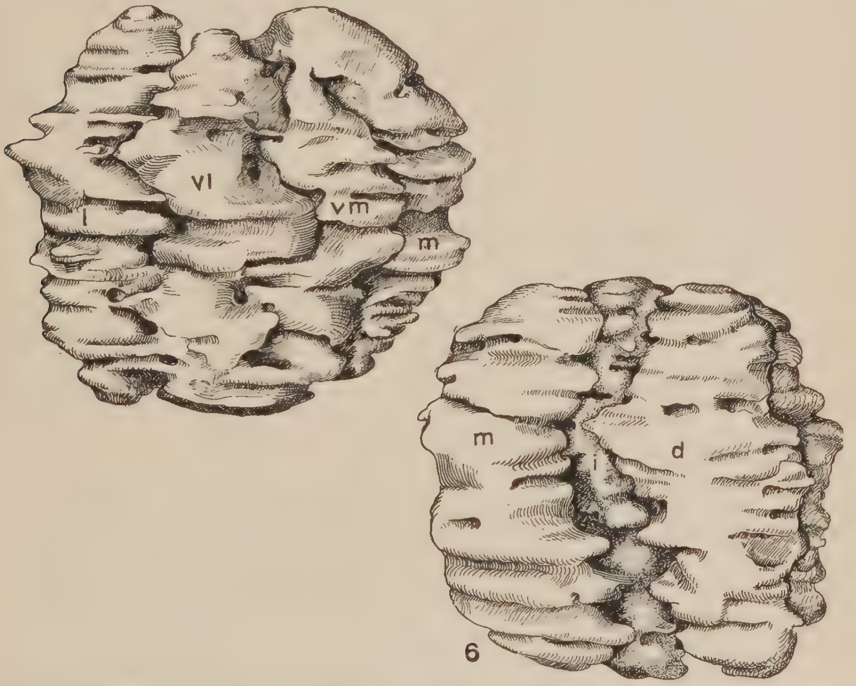

FIG. 144. Wax model of facial nucleus of the cat, × 37. For explanation of letters look under figure 145.

Ventral to the genu and where the genu turns laterally to pass out (fig. 146) the **abducens nucleus** (*an*) will be found in its concavity in the reticular formation. This nucleus gives origin to the abducens nerve (*ab*). The filaments of this nerve spring from the dorsomedial side of the nucleus and curve ventrally to pass through the trapezoid body (*tb*) and out lateral to the cerebrospinal tracts (*cs*). At their curved origin they should not be confused with the fibers of the facial nerve. The abducens nerve supplies the lateral rectus muscle of the eye.

Trace the facial nerve (*f*) from the genu (*gf*) to the surface (fig. 147) and note that lateral to the genu is the medial vestibular nucleus (*mvn*). The curved origin of the direct vestibulo-spinal tract (*vs*) cuts through this nucleus and the facial nerve. Near the exit of the nerve the descending root (*dt*) and nucleus (*tn*) of the trigeminus are on the lateral side; while on its medial side are the rubrospinal tract (*rs*), the ventral spinocerebellar tract (*vsc*) and the lateral lemniscus (*ll*) closely surrounding the superior olive (*so*).

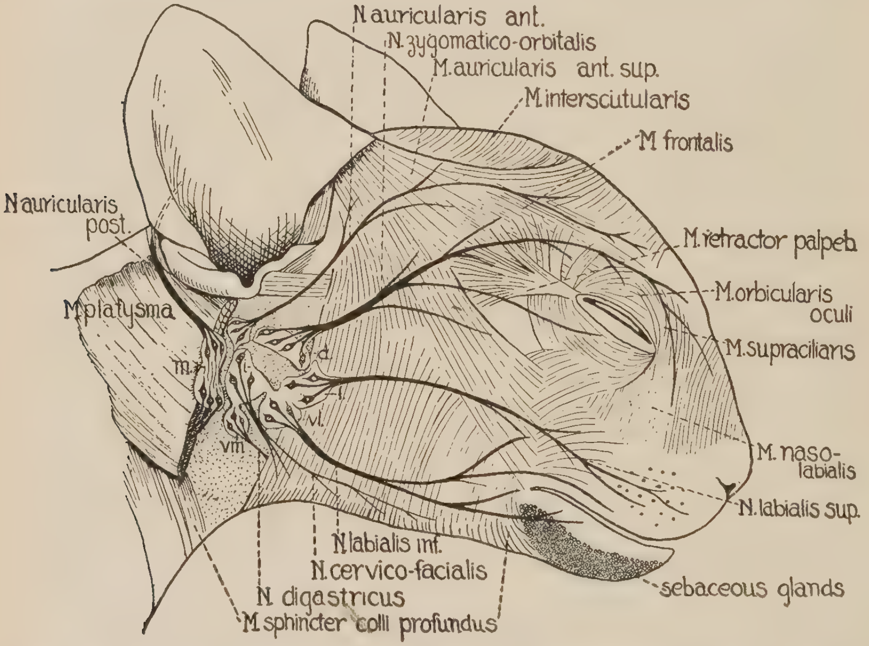

FIG. 145. Schema of origin and distribution of fibers of the facial nerve of the cat. The cell groups of the facial nucleus are projected on the side of the neck. *d*, dorsal group; *l*, lateral group; *m*, medial group; *vl*, ventrolateral group; *vm*, ventromedial group.

Beyond its exit the facial nerve enters the facial canal in the petros part of the temporal bone. In this canal it is joined by the intermedius nerve which we have seen (fig. 142) makes central connections with the upper end of the solitary fasciculus (*sf*) and salivatory nucleus and receives secretory fibers from the salivatory nucleus (*mv*). The intermedius is distributed, through its sensory branch the chorda tympani, to the taste buds of the tip of the tongue while its motor fibers pass to the sublingual and submaxillary glands. Through its greater petrosal branch it reaches the sphenopalatine ganglion and nasal and palatine regions. The facial nerve on the other hand is entirely motor. At its exit it gives a small branch to the posterior belly of the digastric and to the stylohyoideus muscle and then its main trunk is distributed exclusively to all of the muscles of expression of the head, face and neck region. Figure 144 is a wax model of the facial nucleus of a cat. It will be seen that the facial nucleus consists of several groups of cells which form irregular longitudinal columns. Cutting of the various branches of the facial nerve produces chromatic changes in cells of the various columnar groups. In general, each branch supplies a group of facial muscles which have a common or combined action.

This relation of cell groups to branches and to special groups of muscles is schematically shown in figure 145. By cutting separately the nerve branches it has been shown that the large group of small cells that form the dorsal part of the medial (*m*) give rise to the posterior auricular branch that supplies the postauricular and occipital muscles. The cells that form the ventral part of the medial group (*m*) probably supply the platysma. The cells that form the dorsal group (*d*) give rise to the zygomatico-orbital branch and supply the frontal and orbital muscles. The group of cells between the medial and dorsal groups gives rise to the anterior auricular branch and supplies the preauricular muscles. The cells of the large lateral group (*l*) give rise to the superior labial nerve and supply the superior labial muscles. The cells of the large ventrolateral group (*vl*) give rise to the inferior labial nerve that supplies the inferior labial muscles. This group is usually partly joined to the lateral group. The small ventromedial group (*vm*) probably supplies the posterior belly of the digastric. And the large immediate group (*i*) probably supplies the sphincter colli profundus. In regard to its cell groups the facial nucleus of mammals follows a common plan of subdivision associated with the differentiation of the facial musculature and branches of the facial nerve. In figure 145 the facial nucleus is projected on the side of the neck. It shows the relation of the various cell groups of the facial nucleus to the branches of the facial nerve.

The original position of the facial nucleus was close to the dorsal midline. During phylogeny and development it has shifted to a caudal and lateral position to keep in line with the gustatory and motor fiber systems that connect with the masticator and ambiguus nuclei. Its outgoing fibers establish their position before the shifting of the nucleus begins. As this shift takes place the root fibers elongate to form the characteristic internal bend or genu of the facial nerve.

In Selachians the vagus, ninth and hyomandibular (facial) are the nerves that reflexly move the gills in the rapid respiratory movements and the facial nucleus migrates back in line with the ninth. In most of the Teleosts respiratory currents are produced by movements of the operculum which covers the gills. Thus a respiratory opercular mechanism develops which is innervated chiefly by the masticator and facial nerves.

In Mammals the respiratory mechanism is shifted to the vagal centers. The movements of the lips, jaws and pharynx are combined for the ingestion of food. As a result the masticator, facial and ambiguus nuclei are lined up in one column along the ascending gustatory tracts and descending motor tracts.

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CHAPTER 23

INTERNAL STRUCTURE OF THE LOWER LEVEL OF THE PONS, THE VESTIBULAR NUCLEI AND TRACTS

THESE sections (figs. 146 and 147) cut through the levels where the oblongata merges with the pons. Here the most conspicuous features are the cochlear nuclei (*vcn*), the superior olive (*so*) and trapezoid body (*tb*), the facial genu (*gf*) and the vestibular nuclei and vestibular roots.

The ear-like structures that hang over the dorsal and lateral surfaces of the restiform body (*rb*) are the **cochlear nuclei** (*vcn*). In the lower tip of these the cochlear nerve ends. The nuclei consist of two portions; a dorsolateral nucleus or acoustic tubercle (*at*) made up of fine cells and a ventromedial one (*vcn*) made up of larger cells. Between them is a band of fibers, the **acoustic stria** (*as*). Its origin from the cochlear nuclei is seen in figure 142. It passes over the dorsal surface of the restiform body (*rb*) and descending vestibular root (*dvr*) and nuclei (*dvn*). It continues in a medial and forward curve over the vestibular nuclei as seen in figure 143. From this point it disperses into the reticular formation, some of its fibers passing to the superior olive of the same side while others cross the midline dorsal to the trapezoid bodies and reach the superior olive of the other side where they join the **lateral** (auditory) **lemniscus** (*ll*) of the other side. The **trapezoid body** (*tb*) is seen to issue from the medial side of the cochlear nuclei (fig. 146) and pass over the ventral surface of the oblongata to reach the superior olive (*so*) into which it sends many collaterals (fig. 147). Between the superior olives it intercrosses with its fellow of the other side and turns upward around the ventrolateral border of the superior olive as the lateral lemniscus (*ll*). Examine the brain stem on its ventral side and note the origin and course of the trapezoid body (figs. 73, 74).

The vestibular mechanism

In the following study your attention should be confined to the vestibular roots, their nuclei and the tracts to which they give rise. Collectively these are spoken of as the **vestibular mechanism** represented in figure 150. By means of the uncinate fasciculus (*uf*) it is linked up with the cortex of the cerebellar vermis and put under its tonic influence. The vestibular nuclei and tracts become an important dynamic mechanism for keeping up a discharge of excitations into the nerves that supply the muscles. This produces muscular tenseness or static tonus, especially as the muscles are used to resist gravity and maintain posture. The limbs play an important part in posture, hence this mechanism affects the limb muscles as much as those of the trunk, head and neck. The action of this mechanism is relaxed or abolished during sleep or by an anæsthetic such as ether. It is pronounced in decerebrate animals.

In the sections where the restiform body (*rb*) joins the cerebellum (figs. 143, 146) there are seen on its medial side the large cells that constitute the **lateral vestibular nucleus** (*lvn*). Ventral to it is the compact descending vestibular root (*dvr*) and uncinate fasciculus (*uf*). The large cells are separated by coarse fiber bundles which are in reality the great root that the vestibular nerve sends into this nucleus to end upon its cells. A part of this root passes through the nucleus dorsally to end in the posterior lobe of the cerebellar vermis (nodulus, uvula and pyramis). This is the **cerebellar root** (*cr*) of the vestibular nerve (fig. 143). The sharp curve that it makes in a caudal and ventral direction to reach the nodulus and uvula cannot be seen because these parts are omitted from the lower figures.

Follow the **lateral vestibular nucleus** (*lvn*) through the sections and determine its extent and relations. It is distinguished from the other vestibular nuclei by the large size of its cells dispersed by the large root bundles of the vestibular nerve. On the lateral side it is bounded by the restiform body (*rb*) which is here turning dorsally to enter the medullary substance of the cerebellum (figs. 146–147). The **vestibular nerve** (*vn*) is seen to enter as a flat band between the restiform body (*rb*) and descending trigeminal root (*dt*). The compact bundle seen dorsal to the trigeminus is the descending vestibular root (*dvr*) combined with the uncinate fasciculus (*uf*). The vestibular nucleus and the large root entering it as well as the cerebellar root are dorsal to the descending vestibular root. On the medial side is the smaller medial vestibular nucleus (*mvn*) which can be recognized by its small cells and absence of root bundles which gives it a clear appearance. At a higher level larger cells appear in the medial vestibular nucleus (fig. 147). In higher sections (fig. 151) both nuclei diminish in size and soon disappear. Here the descending and cerebellar roots are wanting since they have turned in the other directions, but a superior root (*svr*) of the vestibular nerve is clearly seen passing dorsally into the superior vestibular nucleus (*svn*) under the brachium conjunctivum. Here the uncinate fasciculus (*uf*) emerges on the lateral side where it is seen curving over the brachium conjunctivum (*bc*).

From its medial side the lateral vestibular nucleus (*lvn*) emits the large **direct vestibulospinal tract** (*vs*) of fibers (figs. 146, 147). The origin of this tract is always seen as a prominent wisp of fibers that stream through the medial vestibular nucleus (*mvn*) from the level of the outgoing limb of the facial nerve down to the level of the facial nucleus. Since they turn down into the reticular formation their identity is soon lost. The **acoustic stria** (*as*) should not be confused with this tract as it passes across its dorsal part but with an upward inclination. The vestibular fibers (*vs*) pass beneath the facial genu (*gf*) and through the dorsally going filaments of the facial nerve. Here they turn downwards to form a large **direct vestibulospinal tract** (*vs.*) in the middle of the reticular formation in each half of the oblongata. This tract is seen (figs. 143–147) descending as a condensation of longitudinal fibers in the reticular formation lying between the facial genu and the medial side of the facial nucleus. Followed down in sections the tract shifts ventrally (fig. 140) and comes to lie over the lateral surface of the inferior olive (fig. 135). Then it passes through the upper medial portion of the lateral nucleus (fig. 131). In the lower oblongata it comes to lie quite medial to the main body of the lateral nucleus (130). Where the oblongata joins the cord (129) the tract comes to lie at the ventral surface lateral to the uncrossed cerebrospinal tract and in this position descends throughout the entire length of the cord (fig. 114).

By means of the direct vestibulospinal tract the lateral vestibular nucleus discharges impulses into the motor centers of the cord which maintain or increase the extensor (or antigravity) tonus of the muscles. This function depends on the fact that the lateral vestibular nucleus, like the medial and descending ones, receives a root of the vestibular nerve as well as a large bundle of the uncinate fasciculus (*uf*) from the cerebellum. Through the nerve it receives excitation directly from the acoustic maculae (fig. 157) in the vestibule and semicircular canals stimulated by changes of position of the head. This is the primitive vestibular reflex arc which is normally reinforced by a circuit through the cerebellar cortex. Through the uncinate bundle it receives excitations from the fastigial nucleus which is in turn stimulated by the Purkinje cells of the cortex of the cerebellar vermis. This forms the additional cerebellar circuit.

It has been pointed out in Chapter 21 that the fibers of the restiform bodies such as the spinocerebellar tracts and fibers from the accessory olivary nuclei discharge impulses into the cortex of the anterior lobe, tuber vermis and nodulus, uvula and pyramis. The cerebellar root of the vestibular nerve discharges impulses into the cortex of the nodulus, uvula and pyramis. Great fields of Purkinje cells of the vermis are thus influenced by changes in the position of the head and neck and by changes in the tension in muscles and joints of the trunk and limbs. Their excitations are conducted into the fastigial nuclei, thence by the uncinate bundle to the various vestibular nuclei which are thus enabled to keep up a rate of impulses adequate to **maintain** any appropriate posture or strength of any simple supporting and balancing (antigravity) movement. Animals in which the direct vestibulospinal tract is cut show a marked weakness or atonia and rolling movements on the side of the injury, which they can in time compensate by voluntary effort. The tonic

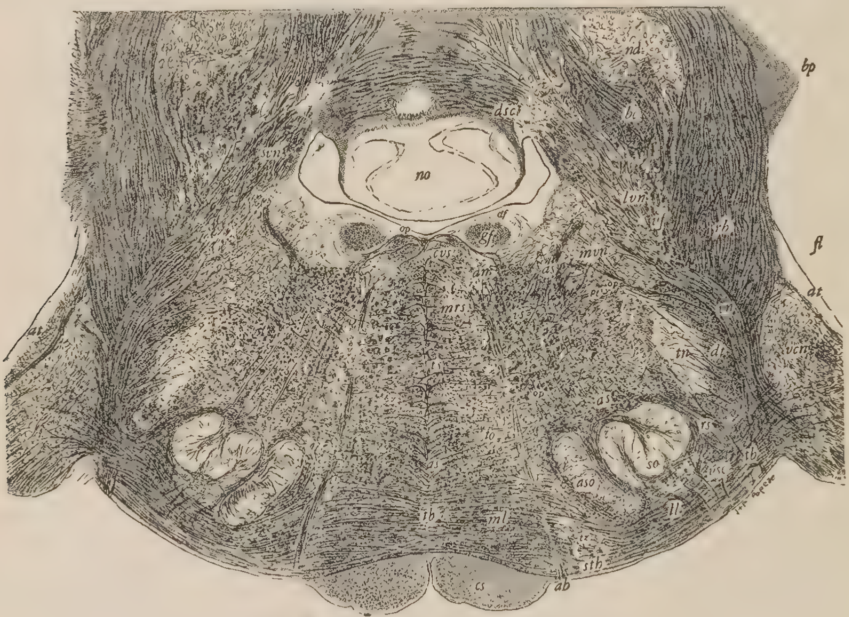

Fig. 146. Section through the superior olive and abducens nerve, × 7.

action of this tract is therefore opposed to the inhibitory influence of the crossed vestibulospinal tract against which it is balanced functionally. Such an arrangement is spoken of as reciprocal innervation. It is illustrated in figure 150. Later study will show that the medial and superior vestibular nuclei and the tracts which they emit exercise a similar influence on the muscles that move the eyes and head.

As the descending vestibular nucleus (*dvn*) is followed upwards in the sections (fig. 135 to 143) it is seen to diminish in size. It becomes reduced to a triangular mass of small cells, the *medial vestibular nucleus* (*mvn*). This lies on the reticular formation between the facial genu and the incoming roots of the vestibular nerve and lateral vestibular nucleus (*lvn*). The vestibular root gives off many fine collaterals that pervade the medial nucleus. Through its dorsal part the acoustic stria (*as*) pass as a dense band. The cells of the medial nucleus emit fibers that pass through the reticular formation ventral to the facial genu, cross the midline and bifurcate into ascending and descending branches. The descending branches join the crossed vestibulospinal tract (*cvs*) while the ascending branches form the **crossed vestibulo-mesencephalic tract** (*cvm*). This passes up as the medial part of the medial longitudinal fasciculus to end in the trochlear and oculomotor nuclei in the midbrain. Cutting of these fibers on one side produces a persistent torsion of the head to the same side.

Now study the connections of the superior vestibular nucleus. A section through the outgoing limb of the facial nerve (fig. 147) cuts through the upper ends of the lateral and medial vestibular nuclei which soon disappear above this level. Here the large **superior root** (*svr*) of the vestibular nerve is seen passing dorsally to end in the **superior vestibular nucleus** (*svn*). This is an oval mass of cells medial to the brachium conjunctivum (*bc*) and in the lateral wall of the fourth ventricle. In Weigert sections it is distinguished by the numerous fine myelinated fibers that pervade it. At this level the uncinate fasciculus (*uf*) can be recognized as it curves over and through the lateral side of the brachium conjunctivum. As its fiber bundles turn down they are seen to take a position between the restiform body and the superior vestibular root. At lower levels (143) they merge with the descending root of the vestibular nerve.

Followed upwards (151) the superior vestibular nucleus is soon replaced by a fiber tract on its medial side, the **direct vestibulo-**

mesencephalic tract (*cvm*). This gradually shifts medially in the floor of the fourth ventricle (fig. 161) to form the lateral horn of the medial longitudinal bundle (*mlf*). In this it ascends to end in the trochlear (fig. 163) and oculomotor nuclei (fig. 165). It will be recalled that the main portion of the medial longitudinal fasciculus at these levels is formed by the crossed **vestibulo-mesencephalic tract** (*cvm*) from the medial vestibular nucleus.

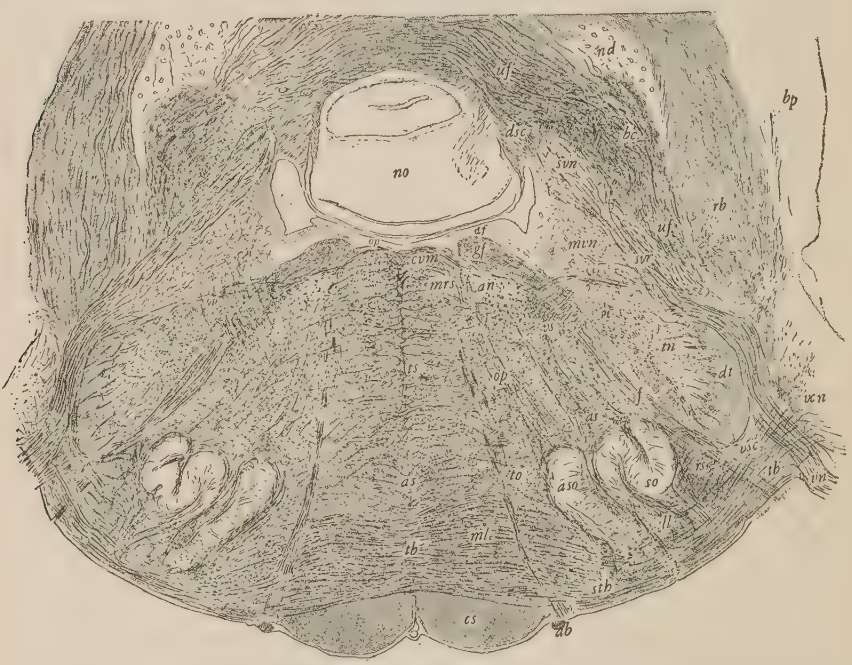

Fig. 147. Section through the region of the outgoing limb of the facial nerve.

These tracts appear to constitute a tonic reciprocal innervation of the eye muscle nuclei for the purpose of supplying tonus and varying the posture of the eye muscles. The direct tract (*vm*) from the superior vestibular nucleus increases their tonus while the crossed tract (*cvm*) from the medial nucleus decreases their tonus. From clinical literature it appears that lesions of the pons, lateral and above the abducens nuclei give a deflection of the eyes away from the side of the lesion. This would be explained as due to the loss of the excitor function of the direct vestibulo-mesencephalic tract and of the inhibitor function of the crossed tract. Experiments on animals support this view. Lesions of the nuclei give rise to oculogyric disturbances, squints and torsions of the head. The functions of convergence and divergence and binocular (conjugate) movements of the eyes in the horizontal as well as vertical planes are performed by the superior colliculi through the tecto-mesencephalic tracts arranged also in the form of reciprocal innervation. The vestibulo-mesencephalic tracts supply only the tonic innervations for this system, that is, the excitations necessary for maintaining the posture of the head and eyes. Experiments on the anterior lobe of the cerebellum indicate that it influences eye movements most likely by impulses through the uncinate fasciculus into the medial and superior vestibular nuclei, and thence by the vestibular tracts to the nuclei of the eye muscle nerves.

Follow out in the sections the roots of the vestibular nerve. It is seen to enter the upper end of the oblongata (fig. 146) as a ribbon-like band. This perforates the origin of the trapezoid body (*tb*) medial to the cochlear nuclei, then passes between the ventral cochlear nucleus (*vcn*) and the descending root of the trigeminus (*dt*). Medial to the restiform body (*rb*) and uncinate fasciculus (*uf*) it gives off its four characteristic roots. The **descending root** (*dvr*) is most ventral passing down (fig. 143) with the uncinate fasciculus (*uf*); and both terminate by numerous collaterals on cells of the descending (*dvn*) and medial vestibular nuclei (*mvn*). The lateral root ends directly in the lateral nucleus (*lvn*), dorsal and lateral to the descending root and medial nucleus. The superior (fig. 147, *svr*) extends upwards and dorsally into the superior vestibular nucleus (*svn*). The **cerebellar root** (fig. 143, *cr*) appears as that part of the lateral root that arches dorsally into the cerebellar vermis. It ends in the cortex of the nodulus, uvula and pyramis. There is also a small **crossed root** which passes under the genua of the facial nerves and ends in the vestibular nuclei of the other side.

The **uncinate bundle** (*uf*) is the large efferent connection of the cerebellar vermis with the vestibular nuclei. It arises in the fastigial nuclei (fig. 143, *fas*) of both sides, passes forward, crosses the midline and curves ventrally over the dorsal surface of the brachium conjunctivum (fig. 147, *uf*) through the anterior border of the dentate nucleus (*nd*). Then it curves down medial to the restiform body but lateral to the superior root of the vestibular nerve (figs. 146 and 147). Several limbs of this bundle radiate into the superior, lateral, medial and descending vestibular nuclei. The long descending limb passes down in the lateral side of the descending vestibular root. The limb to the lateral nucleus is interspersed with the vestibulo-cerebellar root. It is an interesting fact that some of the fibers of the fasciculus descend through the reticular formation with the direct vestibulospinal tract as far as the obex. This observation has led some authors to assign a cerebellar origin to the direct vestibulospinal tract.

Figure 150 represents the central connections of the cerebello-vestibular apparatus. Its composition and theory of function may be summarized:

1. The vestibular nerve (*vn*) enters between the restiform body and descending root of the trigeminus. It gives a root to each of the vestibular nuclei (lateral, medial, descending and superior); a root directly to the cortex of the nodulus, uvula and pyramis of the cerebellum and probably a small crossed vestibular root to the opposite vestibular nuclei. These roots discharge excitations into these nuclei whenever changes of posture stimulate the end organs in the saccule, utricle and ampullae of the semicircular canals.
2. The fibers that constitute the restiform body (*rb*) discharge into the cerebellar vermis proprioceptive impulses from posturally tense (or tonic) muscles. Whenever this tension or posture is altered this discharge is varied. The vermian cortex acts as an excitation field for the fastigial nuclei.
3. The fastigial nuclei (*fas*) give origin to the uncinate fasciculus (*uf*) of each side which discharges these continuous cerebellar excitations into the vestibular nuclei.
4. The lateral vestibular nucleus (*lvn*) gives rise to the great direct vestibulospinal (*vs*) whose fibers end in the motor nuclei of the same side of the cord into which they discharge tonic impulses.
5. The descending vestibular nucleus (*dvn*) gives rise to the crossed vestibulospinal tract (*cvs*) which passes down in the medial longitudinal fasciculus and ends on the motor nuclei of the cord of the other side. Into these it discharges impulses which cause inhibition or diminution of tonus of the muscles of the opposite side.
6. The superior vestibular nucleus (*svn*) gives rise to the direct vestibulo-mesencephalic tract (*vm*) that forms the lateral horn of the medial longitudinal bundle and ends on the nuclei (*tro, om*) that supply the eye muscle of the same side. To these it supplies tonic impulses.
7. The medial vestibular nucleus (*mvn*) gives rise to the crossed vestibulo-mesencephalic tract (*cvm*) that forms the main portion of the medial longitudinal fasciculus and ends on the nuclei (*tro, om*)

that supply the eye muscles of the opposite side. It probably inhibits the tone of these muscles. The descending branches of these fibers probably supply similar excitations to the neck muscles that move the head.

8. If the foregoing functions are correctly assigned, then the small cells of the medial and descending vestibular nuclei emit the crossed ascending and descending tracts whose excitations produce a reduction or inhibition of muscular tonus, whereas the large cells of the lateral nucleus emit the direct or uncrossed tracts whose excitations produce an increase of muscular tonus.

9. The descending root ends at the obex in a special medial part of the accessory cuneate nucleus. This gives rise to arcuate fibers which join the medial lemniscus and end in the thalamus. It is possible that by this means vestibular impulses are conducted cerebralward.

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CHAPTER 24

THE MOTOR SYSTEMS AND REFLEX MUSCULAR FUNCTIONS

THE skeletomuscular system is the chief instrument with which the individual is able to confront his environment and to cope with it effectively. The activities of this system are concerned chiefly with posture and movement; accomplished by the coördinated action of various groups of muscles. The tonic and contractile properties reside in the protoplasmic and chemical structure of the muscle fibers. But these properties of muscles must normally be activated by excitation processes induced in them by nervous impulses in the motor nerves. The maintenance and regulation of these excitation processes in the muscles by means of the motor nerves become one of the most highly organized functions of the nervous system.

Monomuscular reflex arcs. The tonus (or contractile pose), the active contraction and relaxation of every muscle is mediated by means of a sensor-motor arc connected with some part of the central nervous system. The muscles of the limbs and trunk (and neck) are supplied by spinal nerves; and the reflex connections of their sensory and motor fibers take place in the spinal cord. Figure 148 shows the plan of such a **monomuscular arc** for the human biceps muscle, although this arc actually consists of several hundred fibers. It is seen that the sensory fibers arise from cells in the spinal ganglia. Their central fibers form the dorsal roots and end in the cord. Their peripheral fibers end in one or more muscle or tendon spindles (figs. 96 to 99) situated in or at both ends of the muscle. When the muscle contracts or is otherwise stretched the tension of the fibers within the spindles stimulates the sensory fibers that end in it and generates a series of impulses that pass through the fibers to enter the cord. Within the cord the central fibers discharge by means of the direct reflex collaterals (*k*) into the motor cells (*m*) which in turn discharge into the muscles through their motor end plates (figs. 112–113). Sherrington, by degenerating the motor root fibers, has estimated that about three-fifths of the fibers that pass to a long muscle are motor and the remainder sensory.

Every muscle, when it comes to a position of rest, is adjusted against a certain amount of resistance or tension due to the action of gravity or other antagonistic muscles of the body, the limbs, head, jaw, etc. This is particularly true of the extensor muscles of the limbs which resist the force of gravity and thus support the weight of the body. This fixed muscular adjustment is known as plastic or **postural tonus** in contrast to the **contractile tonus** of a muscle when it is shortening or stretching. Postural tonus depends upon a fixed but steady rate of flow of impulses into the muscles through the motor fibers. An increase or decrease of this rate of flow leads to contraction or relaxation of the muscles and a change of pose.

Normally the tonic flow of impulses through the motor nerves is excited from several sources which are summated algebraically in the motor cells, (1) from the afferent muscular nerves, (2) from the fasciculi proprii of other levels, (3) from the vestibulo-spinal, (4) rubrospinal, (5) tectospinal, and (6) cerebrospinal tracts, reinforced by the tonic activity of the cerebellum. When the spinal cord is cut, only the effects of (1) the afferent fibers and (2) the local fasciculi proprii remain, while the effect of the other tracts is completely removed. Such **spinal animals** have lost a large part of their antigravity tonus in the affected limbs which can no longer sustain the weight of the body. When suspended in air such animals can perform in response to appropriate stimuli many of the common natural movements such as movements of running, scratching, defecation, etc. Sherrington has shown that the tonic response through these spinal arcs is directly in proportion to the tension exerted on the muscles. He has given this function the appropriate name of **myotatic tonus.** The monomuscular arcs and spinal centers can indeed cause and regulate a low grade tonus, sufficient to perform complicated movements, but they are unable to give to the muscles that strong, steady and enduring tonus which is necessary for simple standing. When the dorsal roots are cut, these spinal reflexes can no longer be obtained. When the motor nerves are cut the paralysis becomes complete, the muscles become toneless, lengthen and eventually atrophy, since all impulses have ceased to flow into them.

The knee jerk. The tonic action of the monomuscular arcs can also be demonstrated in any person in a muscle at rest. If

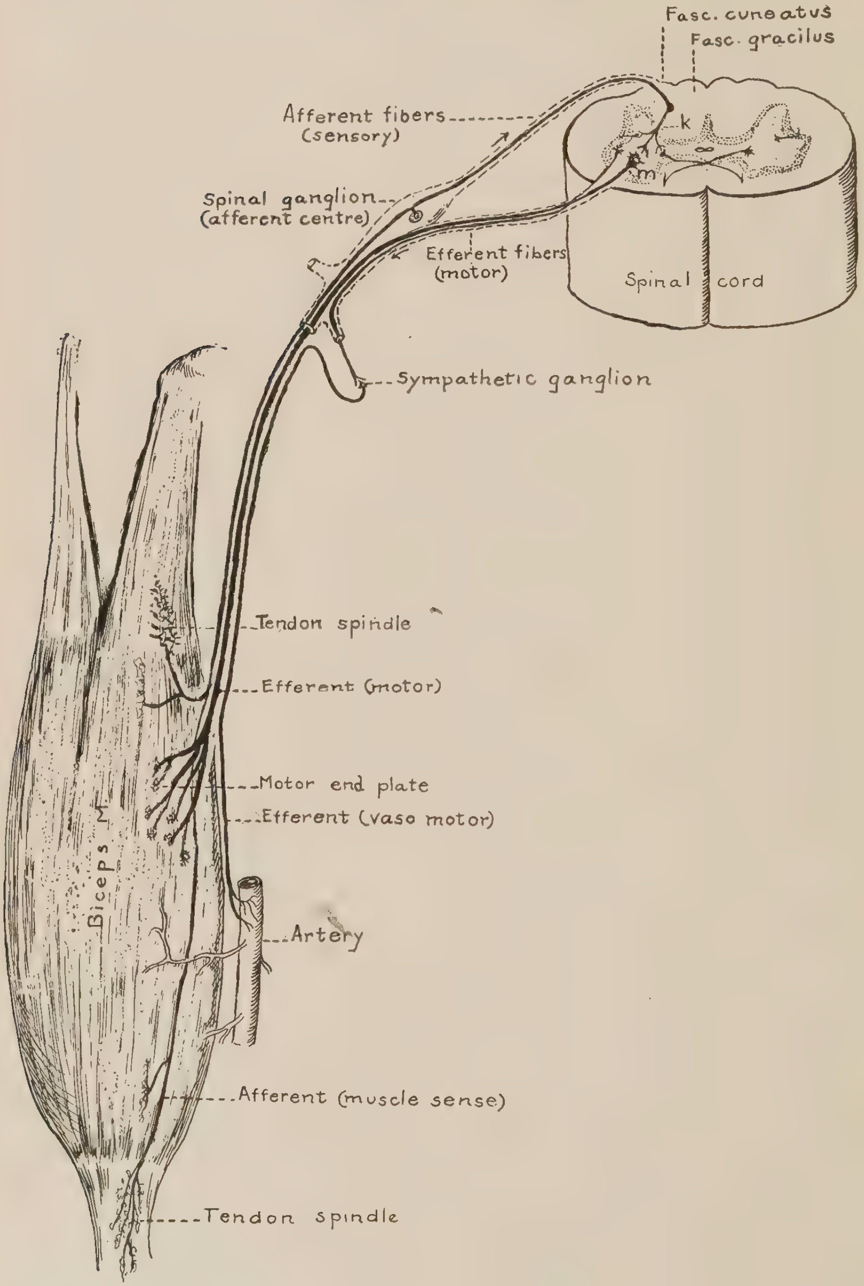

FIG. 148. Schema of a monomuscular arc.

a muscle, such as the quadriceps femoris, is sharply tapped on its patellar tendon when the knee is crossed (fig. 149) the muscle will contract and extend the leg. This is a myotatic reflex, for the degree of extension is proportional to the strength of the tap which, by increasing the tension of the muscle, stretches its muscle spindles. These in turn increase the rate of flow of impulses through its arcs which produces the momentary contraction known as the knee jerk. Such jerks or monomuscular reflexes can be obtained, though less readily, from most all striated muscles of the body whose tendons are accessible beneath the skin. In persons who have suffered a stroke of paralysis resulting in a loss of the cerebrospinal tracts, the monomuscular reflexes become greatly exaggerated in the limbs, and the same results in animals from whom the cerebrum has been removed.

Reciprocal reflex arcs. Over most joints it is usual for several muscles to be allied for the performance of a single movement; and they may in part overlap the next joint. Such an overlap is common in the muscles of the limbs and results in synergy or progressive unity of action. Such allied and synergic groups are usually innervated by closely associated monomuscular arcs. Such groups usually function against similar antagonistic groups, as flexors against extensors or adductors against abductors. The mode of innervation which causes one group to relax, while its opposing group is contracting is known as **reciprocal innervation.** It is mediated by the fasciculi proprii of the cord which unite the monomuscular arcs of various levels (fig. 116).

A plan of the reciprocal innervation of the flexors and extensors of the leg is shown in figure 149; only the number of nerve fibers actually involved runs into thousands. This is the same arc which mediates the knee jerk. It will be seen that the quadriceps extensor group is supplied by its own monomuscular arc through the 2nd to the 4th lumbar nerves. The extensors (hamstring muscles) are supplied by similar monomuscular arcs through the 5th lumbar to the 2nd sacral nerves. The sensory and motor fibers in the monomuscular arcs are linked by direct reflex collaterals in the cord. The opposing monomuscular arcs are linked by the fasciculi proprii (fig. 116).

Other sensory collaterals from the muscular as well as the cutaneous nerves end in the **nucleus of the lateral column** (or intercornual nucleus) which gives rise to the lateral fasciculus proprius in the cord. The reflex fibers (*lp*) from the sacral segments (fig. 149) ascend and end on the motor nuclei for the extensors. The reflex fibers from the lumbar segments descend and end on the motor nuclei for the flexors. So far as is definitely known, the flexor and extensor regions of the same side are connected only by such reflex fasciculi (*lp*) and not by direct fiber arcs. When the flexors are thrown into contraction the extensors relax and vice versa. This is true even where the tendons of the opposing muscles are cut away from their attachments, which proves that the effect is mediated through these spinal reflex bundles. It is natural to assume that this inhibition is carried out by the lateral fasciculi (*lp*) since no other adequate mechanism has been demonstrated in the cord. These reflexes have been extensively studied by Sherrington and others in spinal animals.

Other collaterals of the sensory nerves end in the **intermediate nucleus** (*in*) which gives rise to fibers that cross in the anterior commissure and form the ventral and medial fasciculus proprius (*vp*) of the other side. Thus a crossed innervation of similar groups of muscles is effected which produces either alternating movements such as running, or synchronous movements such as hopping or leaping. Long distance connections exist also between the neck, fore and hind limbs. The lateral (*nlf*) and intermediate nuclei (*in*) of the cord are formed by small multipolar cells (fig. 108) which in many regions greatly outnumber the motor cells. Likewise the fasciculi proprii are formed of a great quantity of fibers. This suggests that reflex inhibition may be produced by a great quantity of stimuli which throws the motor cells into a prolonged refractory state. In the long tracts the effect may be opposite because of a smaller number of fibers.

Cutaneous reflex arcs. The monomuscular reflexes depend on the sensory muscular nerves and the monomuscular arcs. But cutaneous nerves also enter into these arcs, so that many cutaneous stimuli especially from the palms, soles, over flexion areas, etc., give rise to characteristic responses. These are no longer monomuscular or myotatic but purposive. Thus normal stimuli evoke a normal flexion or extension; harmful stimuli evoke protective or defensive movements; pin pricks on the flank evoke a scratch reflex. In addition to the nucleus of the lateral column and the intermediate nucleus, other spinal centers such as the substantia gelatinosa appear to be involved in mediation of these cutaneous reflexes, for they exhibit some other special physiological properties.

Bulbar connections of the spinal reflex systems. The spinal reflex arcs that have been described are not in themselves able to provide the muscles with sufficient excitations to give them steady or enduring tonus sufficient to support the animal even for simple standing. For this purpose functional connections with the bulb and cerebellum are necessary. Several such connections exist as shown in figure 150. (1) Through the spinocerebellar tracts (*vsc*, *dsc*) the afferent nerves of deep sensibility are connected with the

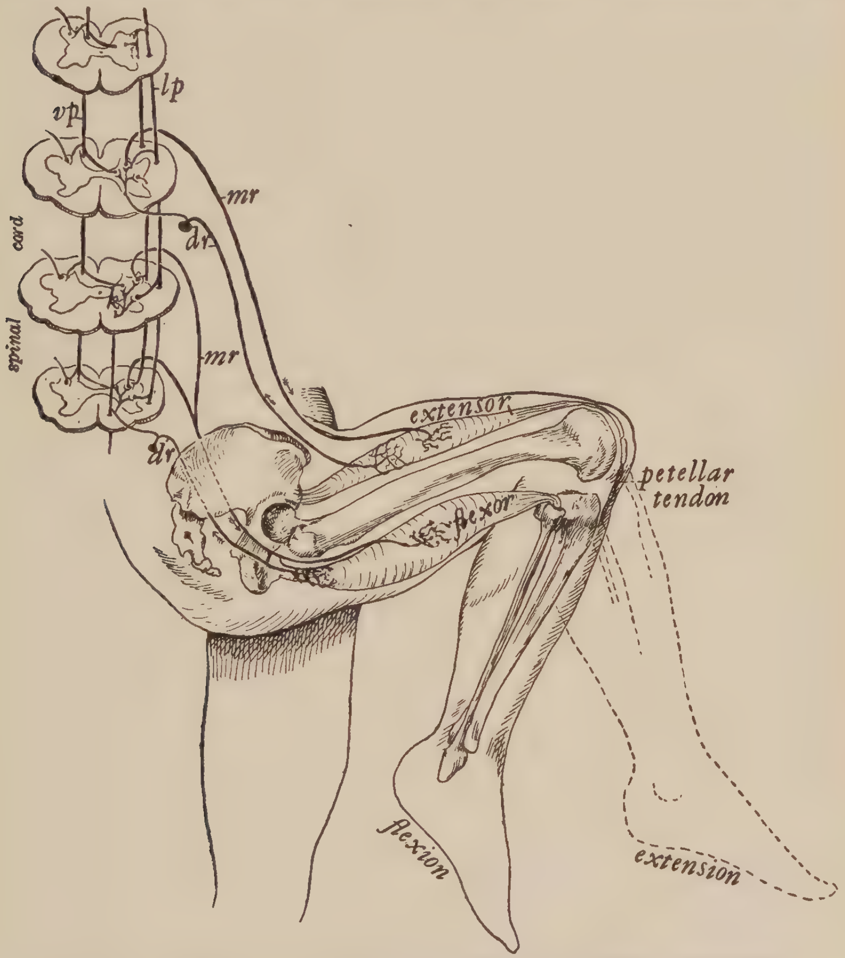

FIG. 149. Schema of the reciprocal innervation of the flexor and extensor muscles of the leg.

cortex of the anterior lobe, nodulus, uvula and pyramis of the cerebellum. (2) The lateral column fibers (*lco*) end in the lateral nucleus of the bulb (*ln*) and the latero-cerebellar fibers (*lc*) relay this connection into the cerebellum, probably into the tuber vermis and lateral lobes. (3) The fasciculi proprii (*lp*) of the neck region end in the accessory olives (*von*) and these in turn relay this connection to the cerebellar vermis.

These three classes of fibers form the restiform body (*rb*) and end on the Purkinje cells (*Pc*) of the cerebellum probably as climbing fibers. Fibers from the cuneate nucleus are often represented as passing to the cerebellum, but this has been denied. The Purkinje cells of the vermis discharge their excitations into the fastigial nuclei (*fas*) and these in turn by the uncinate fasciculus (*uf*) into the vestibular nuclei (*lvn, dvn, svn, mvn*).

The **vestibular reflex system.** The vestibular nerve (*vn*) also excites the vestibular nuclei. It has at least three distinct roots, a root to the lateral nucleus and cerebellum, a superior root to the superior vestibular nucleus and a descending root to the medial and descending nuclei. The lateral vestibular nucleus sends down the **direct vestibulo-spinal tract** (*vs*) that ends on the motor nuclei of the same side. The descending vestibular nucleus whose cells are small and numerous and resemble the intermediate nucleus of the cord sends down the **crossed vestibulo-spinal tract** (*cvs*) that ends on the motor cells of the other side of the cord. In a similar way the superior and medial nuclei supply the nuclei of the eye muscle nerves.

Thus between the cord, the bulb, the cerebellar vermis and vestibular nuclei there exists a closed circuit which exerts a tonic activity on the extensor muscles.

These connections are necessary for the maintenance of the extensor tonus, known as "decerebrate rigidity." If the brain stem is cut across just above the level of the vestibular nuclei this rigidity follows. The standing muscles acquire an abnormally high degree of tonus. These antigravity muscles are the extensors of the limbs, back, neck and tail and the closing muscles of the jaws. The opposing flexor muscles have a low degree of tonus or no tonus at all. Such a decerebrate animal will stand when put on its feet but in an abnormal posture with exaggerated extension of the limbs, neck and tail. The stimuli inducing the enduring tonus of these rigid standing muscles arise chiefly from the muscle spindles of the limb and neck muscles, although the influence of the vestibular organs can also be demonstrated. Such an animal can stand when placed on its feet, it can make slight adjustments to changes in position; but it can neither walk nor respond properly to normal stimuli; when pushed it falls over in helpless rigidity. The distribution of tonus is evidently abnormal.

The **cerebello-rubrospinal reflex circuit** is necessary in order to get a normal distribution of tonus. This midbrain mechanism (fig. 152) is needed in addition to the spinal and vestibular mechanisms just described. To demonstrate the combined action of these mechanisms the cerebrum is removed in order to abolish the cerebropontal and cerebrospinal influences, and the eyes are blindfolded (except in rabbits and guinea pigs) in order to abolish the tectospinal and tecto-olivary influences. In such animals the following reflexes have been demonstrated by Magnus and his associates. To separate the vestibular reflexes from the other proprioceptive and cutaneous reflexes the vestibules have been removed by operation or centrifuging. We will consider first the reflexes that are initiated by the muscle and tendon spindles.

Limb and body reflexes exist in order to carry the weight of the body against the action of gravity. For this it is necessary that the standing muscles shall have, by reflex action, a certain degree of enduring tonus to prevent the body from falling to the ground. In a decerebrate animal in which these lower reflex arcs are intact standing and all kinds of body righting movements are possible. If such an animal is stood on its feet and then one foot is pinched, the stimulated leg is withdrawn from the ground and the weight of the hind part of the body is shifted to the other leg. But this does not yield because its tonus is greatly increased so that it can carry the weight alone.

If an animal deprived of its vestibules be laid on its side on the ground the head will soon assume the normal position. This is due to contact (geotropic) stimuli from the ground. If the stimuli are made symmetrical by laying a weighted board on its upper side then this head righting reflex disappears. These contact stimuli affect the body also. If the head is held in the lateral position the body may be righted as a result of the opposing neck stimuli.

Tonic neck reflexes are also proprioceptive reflexes obtained in a blindfolded, decerebrate animal in which the vestibules have been removed. When the head is moved into various relations to the trunk the tension in the neck muscles is altered. This sets up impulses through the muscular, cerebellar, vestibulospinal and rubrospinal arcs which affect the tonus of the muscles of the limbs and eyes. When the head is bent or rotated to the right side the extensor tonus is decreased in the left limbs and increased in the right; this obviously offsets the shifting of the center of gravity to the right. Raising the head so as to bend the neck backwards causes increased tonus in the fore limbs and reduction of tonus in the hind limbs (except in the rabbit). Such a pose is well seen in a normal cat craning the neck upwards to look on a table. When the head is bent down the hind limbs become more extended and the fore limbs relax as in a cat peering under something or eating food. The latent period of these reflexes is short, being less than one second.

Tonic eye reflexes are also brought into play when the head is moved. They take place in the opposite direction and tend to preserve the original visual field. These limb as well as eye reflexes are abolished by cutting the dorsal roots of the upper three cervical nerves.

Many other reflexes can be cited to show that the muscle and tendon spindles generate impulses through the monomuscular, reciprocal, cerebellar and midbrain arcs which can carry out in an automatic way most of the ordinary standing, walking, running and the body, head and eye righting reflexes without the aid of the vestibule, tectum or cerebrum.

The vestibular reflexes. The vestibule consists of the utricle into which open the three semicircular canals and the saccule which is connected with the utricle by the ductus endolymphaticus. Nerve fibers from the ganglion of the vestibular nerve are supplied to the hair cells that form the end organs (maculae) in each canal, utricle and saccule. The end organ of both utricles is in its floor in a horizontal position when the head is held in the usual normal position. The end organ of each saccule is on its medial wall in a vertical position. Lying among the hairs of the hair cells are crystals of calcium carbonate called otoliths. The otoliths by pulling on the hair cells act as stimuli. They produce the greatest stimulus when they hang and so pull away from the hair cells and least when they press down on the hair cells. The stimuli are continual so long as the position is kept up and give rise through the vestibular tracts to steady reflex tonus while they last. The vestibular nerve discharges these excitations into the various vestibular nuclei which by means of the vestibular tracts distribute them to the motor nuclei for the muscles of the eyes, neck, trunk, and limbs.

Vestibular stimuli are generated chiefly by head movements so the effect of the proprioceptors from the neck muscles can be eliminated either by cutting the dorsal roots of the cervical nerves or putting on the animal a cast so as to immobilize the neck. In such a cast the decerebrate animal can be moved into any position to demonstrate the tonic vestibular reflexes. The most prominent effect is on the limbs, all of which react in a similar way. When the animal is placed on its back so that the mouth cleft is horizontal or vertical the extensor tonus of the limbs is greatest. This is due to the pull which the otoliths exert on the end organs of the utricle which are upside down in this position and their pull is maximal. When the animal is turned legs down so that the head is in a normal position with mouth cleft either horizontal or turned down, the extensor tonus relaxes or falls to a minimum. In intermediate positions the tonus is of intermediate intensity. Similar results are seen when the animal is rotated around the long axis of its vertebral column. When the animal is moved only in the horizontal plane there is no effect on the tonus.

Vestibular reflex eye adjustments occur in all these movements except the horizontal. The eyes keep looking in the direction of the object whatever the movements of the animal. The horizontal deviations are not vestibular but are produced by the tonic neck reflexes. The tonic excitations are distributed to the eye muscle nuclei from the superior and medial vestibular nuclei through the vestibulo-mesencephalic tracts (fig. 150).

Vestibular righting reflexes operate on the neck muscles. As a result the head tends to retain its normal position in space. Visual stimuli must be excluded by blindfolding cats and dogs, which is not necessary in rabbits and guinea pigs. When the animal is held in the air by gripping the pelvis (to avoid lateral contact stimuli) it will be seen that the head tends to retain a normal position in whatever direction the pelvis is twisted or the body is held. This is due to the action of gravity on the vestibular end organs. The latent period of vestibular reflexes is long, usually over ten seconds. When the vestibules or their nerves are cut, these righting reflexes disappear and the head is allowed to drop by the action of gravity.

Unilateral destruction of the vestibule leads to skew deviations of the eyes, nystagmus, rotation and lateral flexion of the head

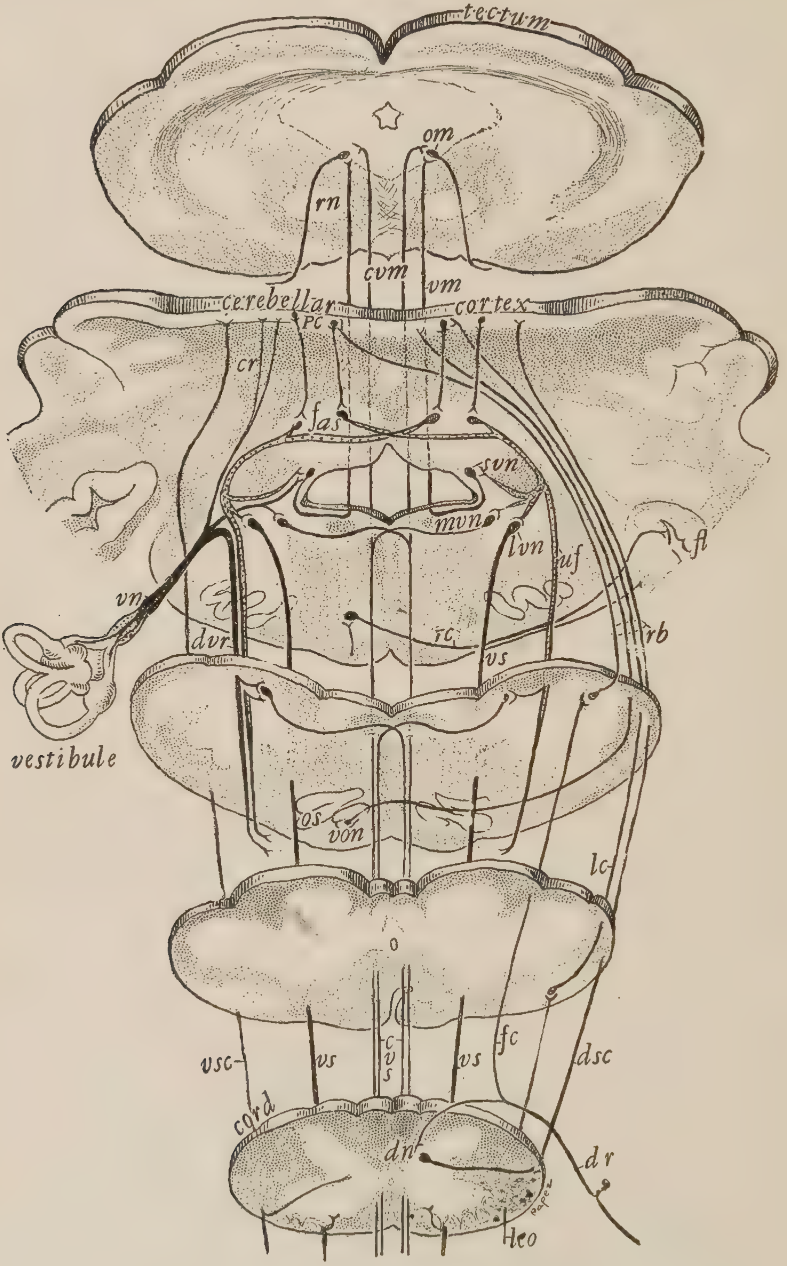

Fig. 150. Schema of the vestibular system.

and also axial rotation of neck and trunk towards the side of the lesion and diminution of tone in the limbs of the same side with an increase in those of the other side. This results in rolling movements in which the animal turns over and over to the operated side. The higher the animal in the scale the less important are the vestibular reflexes. The opossum has highly developed reflex tonus with scarcely any visual or cerebral influence. When a cat is thrown up in the air it always lands on its feet, due chiefly to its vestibular righting reflexes. These are still less important in apes and man in whom vision and muscle sense play a more important part in tonus and in righting and directing the movements of the body.

Tectal reflexes are initiated by light stimuli falling on the retinae. Through the optic nerves light impulses are discharged into the cellular layers of the tectum. Through the posterior commissure and tectomesencephalic tracts which end on the ciliary and oculomotor nuclei, the tectum reflexly directs the muscles of the eyes, to effect divergent and convergent movements of the eyes, and also pupillary and ciliary movements for focusing on close objects. Blinking is another tectal reflex.

The other effect of the tectum is to reflexly change posture or movements of head and of the body and limbs in response to visual stimuli. Such effects are synergized or coördinated with the proprioceptive and vestibular reflexes. The tectum is probably connected with the cerebellum by means of the tecto-olivary tract and olivocerebellar fibers. Cerebellar circuits through the brachium conjunctivum, red nucleus and the rubrospinal tracts are probably called in by tectal functions.

The mechanisms that mediate auditory reflexes are entirely unknown though they are supposed to be effected through the inferior colliculus and superior olive.

From what has been said it follows that normal posture and tonus are largely controlled by the proprioceptive and vestibular arcs, but that alterations of posture and movement are, in the higher mammals, initiated and directed by impressions received through the senses of sight and hearing. Take the example of a cat that hears a mouse moving on his right. Through the auditory reflex tracts the head is turned to the right. As a result of the tonic neck and vestibular reflexes there follows an increase of tonus in the muscles of the right side which preserves the balance by assuming the weight on the right limbs. Because the left limbs are less loaded they will now be the first to move when the cat springs at the mouse. In primates the influences of the striatum and cerebrum are more important.

From what has been said it will appear that proprioceptive, tactile, vestibular, cerebellar, tectal, striatal and cerebral arcs are involved in the order given in the production of the normal distribution of tonus for posture and particularly movement. Those at the lower level are primary parts of the whole mechanism. It has been shown by Magnus that they summate algebraically and that more and more complicated movements ensue with the use of each additional one. All these arcs, however, are merged into a unified motor apparatus that exercises its integrated influence on the motor neurones which provide the final common path for the impulses to the muscles. The number and rate of impulses that reach the muscles determine their degree of contraction or relaxation which is their postural or contractile tonus. The striatal and cerebellar systems are nowhere directly connected with the motor nuclei; but all the other systems have in addition to their extracerebellar reflex arcs also a circuit through the cerebellum (see page 265).

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CHAPTER 25

THE CEREBELLAR BRACHIA AND NUCLEI

SECTIONS through the region of the pons are distinguished by the thick cerebellar brachia or arms which enclose the lateral and dorsal sides of the fourth ventricle. Their relations as they enter the cerebellum may be seen on a single section (fig. 146, *rb, bc, bp*. See also figure 72).

The **restiform body** (*rb*) or inferior brachium has already been traced (page 208), but its entrance into the cerebellum should be followed again. It lies dorsal to the descending trigeminal root (*dt*). Where the restiform body turns dorsally to enter the cerebellum it passes between the brachium pontis (*bp*) and vestibular nuclei (*lvn*). It then curves medially over the outer surface of the dentate nucleus (*nd*) to enter the medullary substance of the upper vermis. The **uncinate fasciculus** (*uf*) is seen on the medial side of the restiform body, describing a similar curve, but passing through the dentate nucleus and through the brachium conjunctivum (*bc*).

The **dentate nucleus** (*nd*) is seen within each side of the cerebellum in sections that pass through the lateral vestibular nucleus (fig. 143 *lvn*). It is a large, thick folded plate of cells dorsal to the lateral vestibular nucleus (*lvn*) and restiform body (*rb*) from which it is separated by the peduncle of the flocculus (*pf*). On its medial side the cerebellar root of the vestibular nerve (*cr*) separates it from the **fastigial nucleus** (*fas*) seen in the roof of the fourth ventricle. In Primates the small emboliform and globossal nuclei are formed between the fastigial and dentate nuclei. As the dentate nucleus is followed upwards a tract of fibers, the **brachium conjunctivum** (*bc*) is seen to gather in its center. The uncinate fasciculus (*uf*) and the vestibular root (*cr*) cut through the dentate nucleus as well as through the brachium conjunctivum. On the lateral side is the restiform body entering the cerebellum. In a section through the outgoing limb of the facial (fig. 147, *f*) the superior vestibular root (*svr*) and nucleus (*svn*) are seen ventral and medial to the brachium conjunctivum. The dentate nucleus (*nd*) is diminishing in size while the brachium (*bc*) is increasing and the uncinate fasciculus (*uf*) is curving through them ventrally as a scattered bundle.

The mass of fibers seen on the outside of the restiform body form the **brachium pontis** (*bp*). The brachia pontis project out on each side and on account of their slanting position (fig. 151) they are cut obliquely in transverse sections. They enter the medullary substance of the cerebellum at the lower level of the pontal region (fig. 147). Here they appear lateral to the restiform body. Against their lower borders are crowded the ventral cochlear nuclei (*vcn*) and dorsal to these the flocculus (*fl*). The fibers that constitute the brachia pontis spread out in the medullary substance and enter the cortex of the lateral or ansiform lobes.

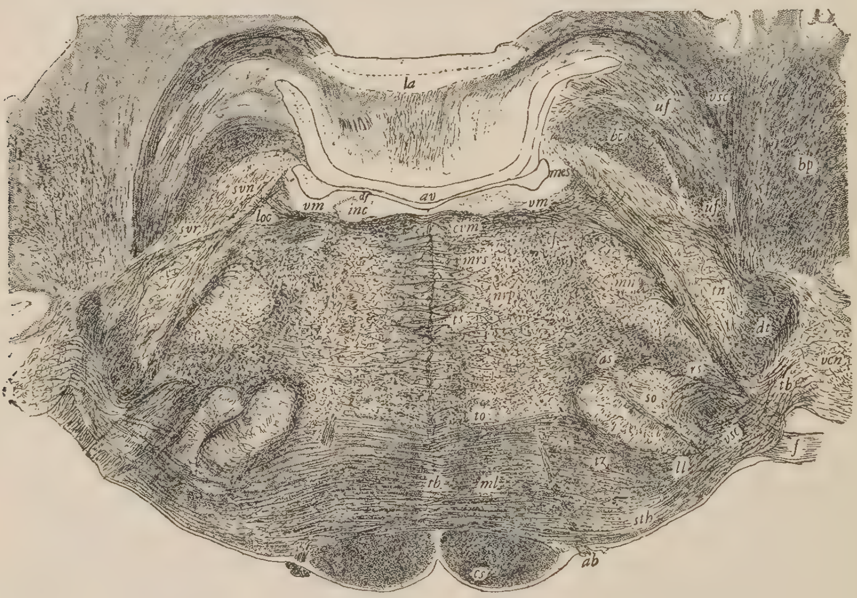

FIG. 151. Section of the pons through the level of the masticator nucleus, × 7.

In the higher sections (fig. 151) the dentate nucleus disappears and is replaced by the brachium conjunctivum (*bc*) now semilunar in shape. Ventral to it is the superior vestibular nucleus (*svn*) and the superior vestibular root (*svr*) entering it. Closely ventral to the vestibular fibers are seen fibers of the trigeminus passing in the same direction to the main pontal trigeminal nucleus that lies ventral to the superior vestibular nucleus. These trigeminal connections should be distinguished from the vestibular root. Here, scattered bundles of fibers can be seen leaving the medial side of the superior vestibular nucleus. This is the direct vestibulo-mesencephalic tract (*vm*) that soon curves medially and forward to form the lateral horn of the medial longitudinal fasciculus higher up. It passes across the lower end of the mesencephalic root (*mes*) of the trigeminus where this is turning dorsally. The brachia conjunctivum (*bc*) are united by the anterior medullary velum (*av*). Curving over the brachium conjunctivum are seen the restiform fibers. The ventral spinocerebellar tract (*vsc*) here describes a dorsal curve across the lateral surface of the brachium conjunctivum to join the restiform fibers and enter the cerebellum.

Where the brachium conjunctivum (*bc*) passes dorsal to the masticator nucleus (fig. 161, *mn*) numerous fiber bundles are seen passing from the brachium towards the oral surface of this nucleus, and possibly as far down as the facial nucleus. It has not been established that the cerebellum actually sends fibers directly to any of the motor cranial nuclei.

The emboliform and globossal nuclei are differentiated in Primates in whom the anterior lobe is greatly enlarged. Their fibers pass forward in the brachium probably to the red nucleus.

The **brachia pontis** (*bp*) form projections on the outside. They are here perforated by the roots of the trigeminus and the masticator nerves (fig. 151, *dt*, *mn*). As the brachia pontis extend in a ventral direction they enclose the pontal nuclei (*pn*) within the prominent pontal protuberance (*pp*). The protuberance and pontal brachia are extremely large in the Primates and extend down to cover over the trapezoid body (*tb*) which in the lower mammals is seen exposed on the ventral surface back of the pontal protuberance.

The **pontal nuclei** (fig. 161, *pn*) are the great gray masses, pierced by columns of longitudinal fibers, the **cerebral peduncles** (*cpo*), cut across in the sections. The cerebrospinal tracts (*cs*) pass through to run along the ventral surface of the oblongata. The fronto- and parieto-pontal fibers (*cpo*) end in the nuclei of the pons (*pn*); so that the sections through the upper level of the protuberance will show great numbers of both sorts of fibers while sections through the lower level will show mostly the cerebrospinal tracts (*cs*). Experimental work has shown that the **fronto-pontal** fibers enter near the midline and that the **parieto-pontal** fibers occupy a lateral position, while the **cerebrospinal** fibers (*cs*) keep an intermediate position. The cells of the pontal nuclei are small multipolar structures on which the fronto-pontal and parieto-pontal fibers end. The cells give rise to fibers that cross the midline and enter the brachium pontis (*bp*) of the other side to end in the lateral lobe of the cerebellum (chap. 10, *ans*).

Through these connections the left cerebral cortex discharges excitations into the right lateral lobe (*ans*) of the cerebellum, and the right cerebral cortex into the left. This follows the principle that the cerebral hemispheres have a crossed connection with all the lower sensory as well as motor centers.

Structure of the upper pontal and isthmic region

Sections through the masticator nucleus (*mn*) and isthmic region should now be studied (figs. 151 and 161). The **brachium conjunctivum** (*bc*) forms the dorsal lateral wall of the ventricle. Over its lateral surface curve the **uncinate fasciculus** (*uf*), and higher up, the ventral spino-cerebellar tract (fig. 161, *vsc*). The **mesencephalic root** (*mes*) of the **trigeminus** is a small bundle medial to the brachium conjunctivum. It comes from the globular cells scattered along its course in contact with it. The root joins the trigeminus and is believed to be sensory and supply muscles of mastication (Willems, Allen). It also sends down a tract of fibers to the salivatory nuclei known as Probst's tract (*Pt*); but it is possible that Probst's tract arises from the locus (*loc*). The large clusters of cells in the angle of the ventricle form the **nucleus of the locus caeruleus** (*loc*). This nucleus receives a small sensory root from the trigeminus (Cajal and Lorento de No). In the human brain the cells of the locus are deeply pigmented and very conspicuous. They give rise to a tract of fibers (at first diffuse and triangular in outline) that passes down in the floor of the fourth ventricle, over the masticator nucleus and joins the acoustic stria of which it appears to be the upper one. It curves to the midline and passes ventrally along the raphe to end possibly in the arcuate nuclei. It may be an afferent connection of the trigeminus system to some part of the cerebellum. Under the brachium conjunctivum (fig. 151) is seen the superior vestibular nucleus (*svn*) which gives origin to the direct vestibulo-mesencephalic tract (*vm*).

The **masticator nucleus** (*mn*) is an oval cluster of large motor cells that give rise to the masticator nerve, or motor *V*, that supplies all muscles of mastication. The nerve root arises from the lateral side of the nucleus and passes out between the masticator nucleus (*mn*) and **pontal trigeminal nucleus** (*tn*). This latter has the characteristic cell clusters such as are seen in the nucleus cuneatus. It is closely related to the masticator nucleus and sends a tract of arched fibers ventrally into the medial lemniscus of the other side. In addition it sends a large **trigemino-thalamic tract** upwards into the central tegmental bundle (*cf*) which can be followed through the midbrain into the nucleus reuniens (*reu*) and ventral nucleus (*ven*) of the thalamus. Around the ventral and medial side of the masticator nucleus is a large tract (*stp*) that chiefly ends in it. This tract arises in the globus pallidus, comes down with the lateral pes lemnisci and rubrospinal tract and ends in the masticator and facial nuclei. It appears to be the loss of this bundle that causes the gaping mouth and paralyzed jaw following lesions of the globus pallidus. It is probable that the pontal trigeminal nucleus sends fibers up into the medial longitudinal fasciculus (Wallenberg). It is likely that sensations from the eye muscles pass along this arc to reach the oculomotor nuclei.

In the **reticular formation** medial to the masticator nuclei are seen large scattered cells that together form the pontal **reticular nucleus** (*nrp*). They give origin to the large **medial reticulo-spinal tracts** (*mrs*) that pass down as the lateral parts of the medial longitudinal fasciculus and are partly crossed (fig. 153). A small special crossed tract, the **lateral reticular spinal tract** (*lrs*) arises in this region, crosses and passes down through the center of the reticular formation to join the rubrospinal and crossed cerebrospinal tracts in the cord.

In the cat Lewandowsky has described a **tecto-olivary tract** (*to*) which is probably identical with the large **thalamo-olivary tract** of the human brain. In the cat it arises from the large central gray mass (fig. 165, *teg*) that surrounds the central tegmental tract in the region of the midbrain and ends in the inferior olive. In the human brain this tract is large and dense and forms a prominent feature of the pons and isthmus. Lateral to it is the **superior olive** (*so*) surrounded by the **lateral lemniscus** (*ll*) and **rubrospinal tract** (*rs*). In the ventral part of the reticular formation that lies on the large pontal nuclei is the densely staining **medial lemniscus** (fig. 151, *ml*).

The **reticular tegmental nucleus** (*nrB*) of Bechterew is the large scattered gray mass at the midline around the medial border of the medial lemniscus (fig. 161). The part that extends dorsally along the midline is the central reticular nucleus (*nrc*). A great number

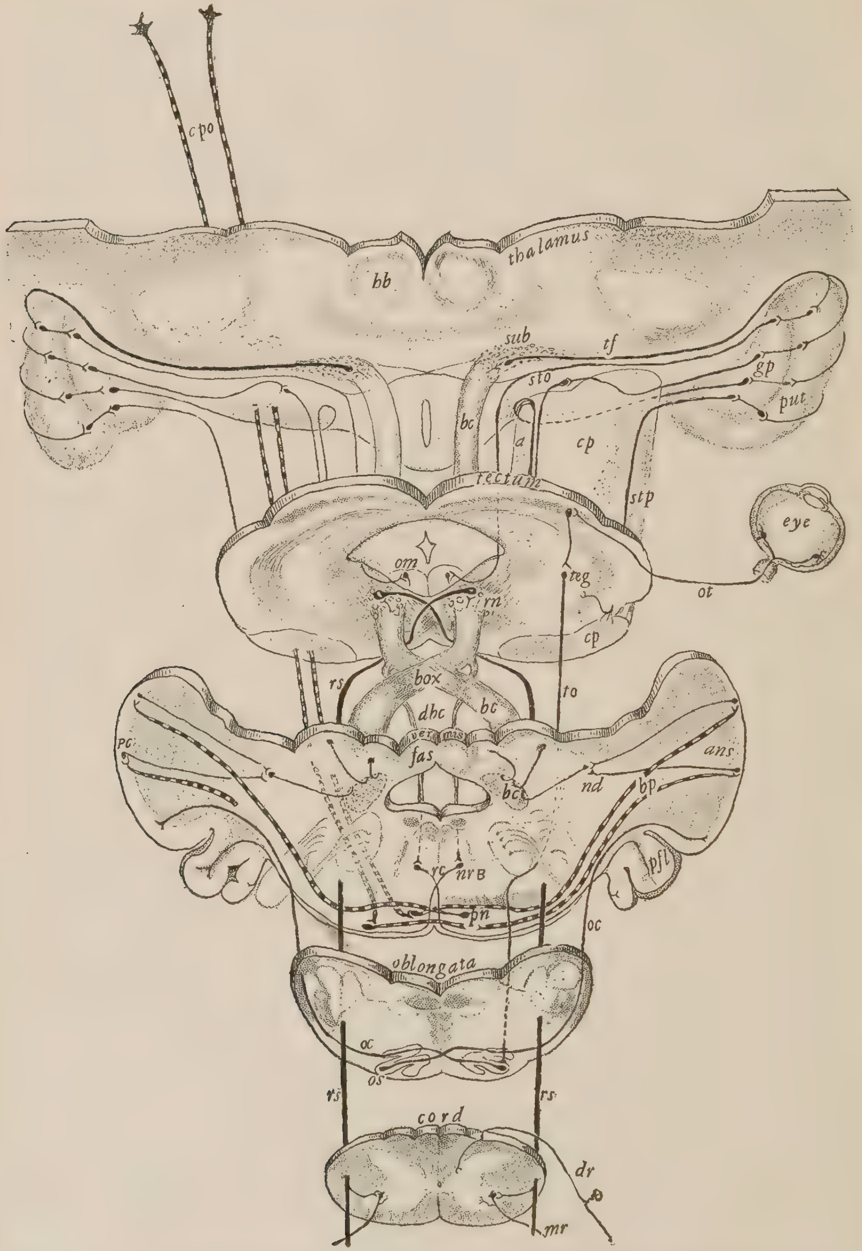

FIG. 152. A plan of the cerebral, striatal and tecto-olivary connections of the lateral lobes of the cerebellum.

of **reticulo-cerebellar** fibers (*rc*) leave these nuclei, cross in the raphe where they form a dense bundle which passes ventrally and then laterally beneath the medial lemniscus. They form the deep stratum of pontal fibers (*rc*) and pass to the cerebellar cortex. The **descending limb of the brachium conjunctivum** (*dbc*) ends in the reticular nuclei. It is a large bundle that comes down from the decussation of the brachium (fig. 152, *bcx*) and forms a heavy stratum over the medial lemniscus (fig. 161) near the midline.

It seems that other fibers coming from the hypothalamus pass through the medial fiber capsule of the red nucleus (fig. 165, *rn*), then through the conjunctival decussation (fig. 163, *bcx*) and end also in these reticular nuclei (fig. 162, *nrB*). They are probably the mammillo-tegmental tract of Gudden. Functionally the hypothalamic reticulo-cerebellar and the reticulo-spinal connections are problematic. They are a primitive system constant in all vertebrates which probably deal with some of the vital functions such as respiration, vascular tone, heat production or metabolism.

The **tecto-spinal tracts** (*ts*) are seen on each side of the central reticular nucleus (*rnc*). On their way down they have to pass over the conjunctival decussation (*bcx*). Along the dorsal midline is the medial longitudinal fasciculus (*cvm, vm*) which on account of its density can be easily distinguished from the tectospinal tract (*ts*). Its main body of each side consists of the **crossed vestibulo-mesencephalic tract** (*cvm*) from the medial vestibular nucleus (fig. 150, *mvn*) while the lateral horn consists of the direct vestibulo-mesencephalic (*vm*) from the superior vestibular nuclei (*svn*). Both end higher up in the trochlear (*tro*) and oculomotor nuclei (*om*). Lateral to these is the central tegmental bundle (*cf*) which is now large, due to the addition to it of the large trigemino-thalamic tract. Ventral to this is the tecto-olivary tract (*to*) which is lost from view in the region of the brachial decussation.

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Midbrain connections of the cerebellum

Follow now the brachium conjunctivum (*bc*) and the pontal protuberance (*pp*) upwards through the isthmic region and midbrain. The brachium conjunctivum sinks into the reticular formation ventral to the inferior colliculus (fig. 162). It comes to lie medial to the lateral **lemniscus** (*ll*) which is here turning dorsally to enter the inferior colliculus (*ic*). The nucleus of the lateral lemniscus (*nll*) is sending many fibers through the brachium (*bc*) across the reticular formation to the inferior colliculus of the other side. This is the commissure of the lateral lemniscus (*cll*). Ventral to the brachium is the **rubrospinal tract** (*rs*) lying also in the medial side of the lateral lemniscus. It must be distinguished from the lateral lemniscus and from the brachium conjunctivum. At lower levels the rubrospinal tract (*rs*) passes on the ventral side of the masticator nucleus (fig. 151, *mn*) lateral to the superior olive (*so*) from which level down it is closely associated with the ventral spino-cerebellar tract (*vsc*). Now follow the rubrospinal tract (*rs*) upwards through the midbrain with the brachium conjunctivum (*bc*). Both will cross over to enter the red nucleus (fig. 152).

The intercrossing of the brachium conjunctivum (fig. 163, *bcx*) is a prominent feature in the reticular formation of the midbrain (tegmentum) especially in the Primates on account of its large size. The fibers of each brachium curve ventrally and cross through each other in a transverse direction and then turn forwards as a round bundle to enter the red nucleus (*rn*). The rubrospinal tracts (*rs*) curve medially and upwards under the ventral surface of this intercrossing, turn dorsally along the midline and intercross (*rsx*) at a higher level between the red nuclei (fig. 165). Their intercrossing (decussation) is therefore above that of the brachium. Dorsal to the **red nucleus** (*rn*) is the intercrossing of the **tectospinal tract** (*tsx*) which is taking place between the red nuclei on a more dorsal level.

The **red nucleus** (*rn*) of each side is an elongated oval mass in the reticular formation of the midbrain, ventral to the superior colliculus or tectum. The red nuclei are easily distinguished by the large size of some of their cells and their round contour in sections. They are enveloped by fiber bundles, the most distinctive of which is the medial longitudinal fasciculus on the dorsal side. The oculomotor nerves (*om*) pass through them in a ventral direction. The brachium conjunctivum (*bc*) is seen passing upward as scattered bundles through the interior of the red nucleus, in which its fibers partly end. A considerable part of its fibers pass beyond to end in the **reticular nucleus of the sub-thalamus** (*sub*) which permeates the pennant-like fiber field (Forel's field 1) above the level of the red

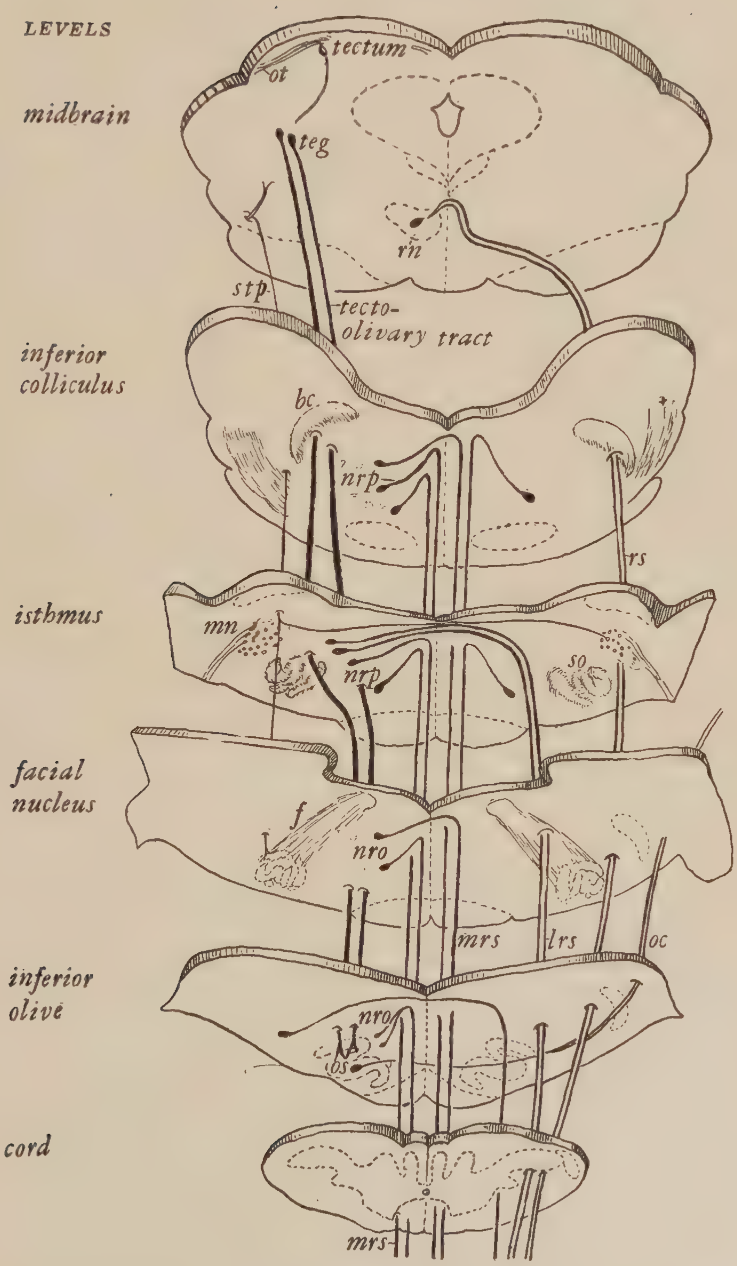

FIG. 153. Diagram of reticulo-spinal tracts in the cat.

nucleus. This field of fibers is formed chiefly by fibers of the brachium conjunctivum and of the thalamic fasciculus (*tf*), an important fiber tract that connects the reticular subthalamic nucleus with the corpus striatum (*put*). Great importance is assigned to the red nucleus since it receives the terminals of the brachium conjunctivum and emits the rubrospinal tract and thus serves as an important arc for transmitting excitations from the lateral lobe of the cerebellum (*ans*) down to the lower motor centers. This is the important cerebellar arc which regulates the stato-kinetic tonus of muscles and tonus during muscular movement whether reflex or voluntary balanced against the extensor tonus mediated by the vermis, uncinate fasciculus and vestibular tracts.

The **rubrospinal tracts** (*rs*) should be traced downwards from section to section. They arise from the cells of the red nucleus, intercross between the red nuclei (fig. 165, *rsx*). Then they curve downwards and laterally, ventral to the crossing brachia conjunctiva (fig. 163). They pass outward from the latter and take a position in the medial border of the lateral lemniscus (fig. 162). They pass ventral to the masticator nucleus (fig. 151) where they become associated with the ventral spino-cerebellar tract. Together these tracts (*rs*, *vsc*) lie lateral to the superior olive (fig. 146), facial nucleus (fig. 142) and lateral nucleus (fig. 130). In the cord they pass down in the lateral column ventral to the crossed cerebrospinal tract (fig. 114). A plan of the rubrospinal tracts is shown in figure 152 (*rs*).

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CHAPTER 26

CELLULAR STRUCTURE AND MECHANISM OF THE CEREBELLAR CORTEX

How the cerebellar cortex may serve as a dynamic field for the production, the increase and decrease of tonic excitations of muscles can be realized only from a study of its cellular structure.

Sections of the cerebellar cortex stained with haematoxylin and eosin, methylene blue, Cajal silver impregnation and Weigert myelin stain should be studied. Note that the core of each folium or gyrus consists of **white substance,** or nerve fibers (*F*). These fibers are (1) the moss fibers (*moss*) from the restiform body, (2) the climbing fibers (*cli*) from the brachium pontis, both coming in to end in the cortex, and (3) the axones (*a*) of Purkinje cells (*Pc*) passing to the dentate nucleus (*nd*) and the other roof nuclei (*fas*). Observe that the **cortex** of the folium consists from within out of three distinct layers, the **granular layer** (*G*), a **layer of Purkinje cells** (*Pc*) and the **molecular layer** (*M*) on the surface (fig. 154). The **granular layer** (*G*) appears as a dense layer of nuclei clearly seen in haematoxylin and methylene blue sections. In silvered sections (fig. 155) each nucleus is seen to represent a single small **granule cell** (*g*). The **moss fibers** (*moss*) terminate among these cells by several moss tufts. The granule cells give off several short dendrites that end in claw-like terminals which are clenched into the mossy tufts of the moss fibers. These connections as seen in sections form small ball-like areas of densely intermingled fibers and are spoken of as glomeruli (*gl*). They occur in vast numbers throughout the granular layer and they constitute the most extensive afferent connections of the cerebellar cortex. Cajal is of the opinion that the moss fibers (*moss*) come from the restiform body (*rb*) and the climbing fibers (*cli*) from the brachia pontis (*bp*) but other authors have produced evidence to support the reverse view.

From each granule cell a slender **axone** passes into the molecular layer where it divides into two fine **tangential fibers** (*tang*) that run in the molecular layer (*M*) along the length of the folium, that is, from side to side in the cortex (fig. 156). These fibers are strung on the spurs or thorns of the dendrites (*d*) of the Purkinje cells (*Pc*). By this means the impulses brought in by the moss fibers are distributed widely through the folia and reach a large series of Purkinje cells. The finely granular nature of this layer (*M*) is derived from the great quantities of fibers (*tang*) from the granule cells as well as the arborizations (*d*) of the Purkinje cells. These arborizations of the Purkinje cells are spread out across the folia, that is, in a sagittal plane, whereas the tangential fibers of the granule cells pass along the length of the folia and form contacts with the branches of a long series of Purkinje cells through which they cross.

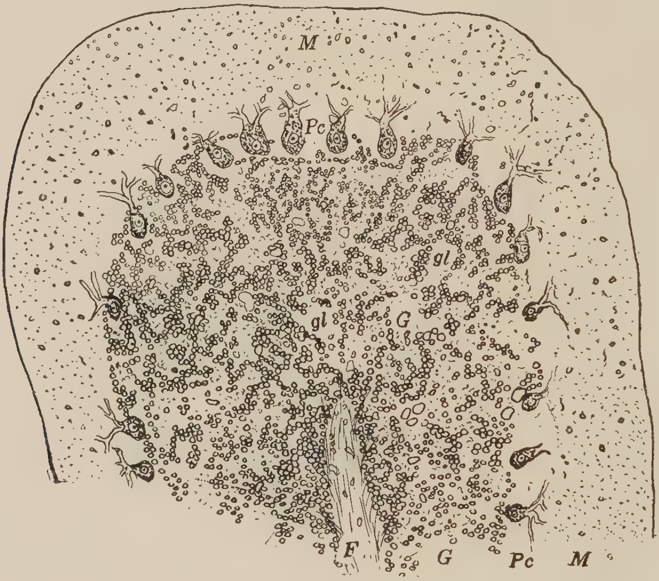

FIG. 154. A section of the cerebellar cortex of a cat. Nissl stain.

A single layer of large **Purkinje cells** (*Pc*) is spread throughout the entire extent of the cerebellar cortex. Their bodies lie close to the granular layer (*G*). They give off one or two stout, densely branching and spiny **dendrites** (*d*) that penetrate the entire thickness of the molecular layer (*M*). These branching dendrites are spread transversely to the folium like a vine on a flat trellis, that is, their spread is in a sagittal plane. Passing through these branches are the tangential fibers (*tang*) of the granule cell (*g*) which form contacts with the spines. Each Purkinje cell is thus in functional relations with hundreds of granule cells in the same folium to both sides of it. The molecular layer may be looked upon as a great synaptic field through which the moss fibers join the granule cells which discharge their excitations into the dendrites of the Purkinje cells. Whether these inhibit or excite the Purkinje cells is not known, but electrical stimulation applied to the surface of the cortex abolishes decerebrate rigidity and suggests an inhibitory function for the molecular layer.

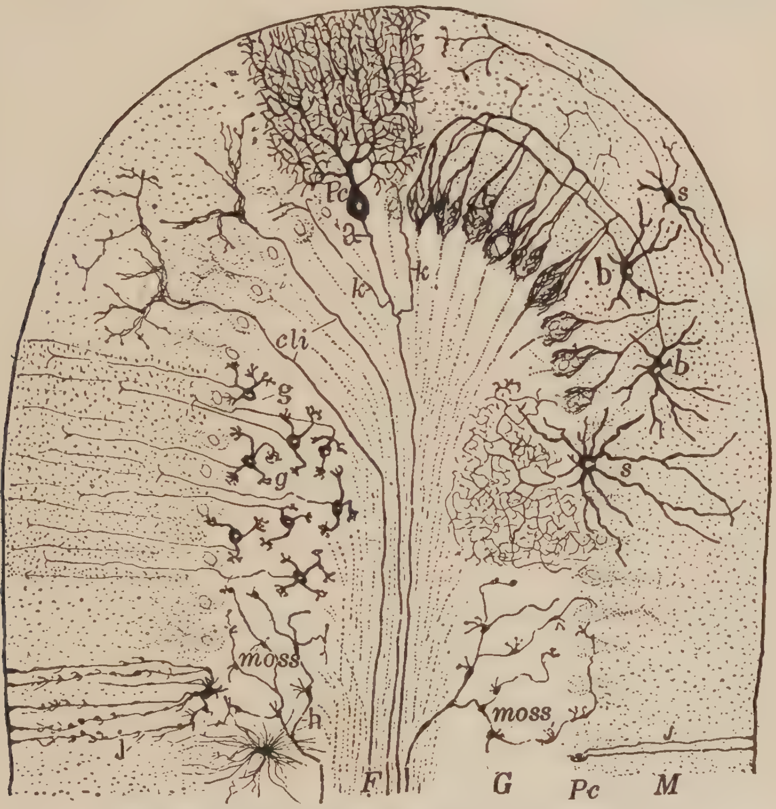

FIG. 155. Cells of the cerebellar cortex. After Cajal.

Another important afferent connection with Purkinje cells is established by the **climbing fibers** (*cli*). Each Purkinje cell has at least one such fiber passing over its body and twining along its dendrites (fig. 155) with which it makes many contacts. The source of the climbing fibers is uncertain but it seems likely that they come from the brachia pontis. They may provide the mechanism for exciting the Purkinje cells.

The **basket cells** (*b*) are small cells scattered among the Purkinje cells. Their dendrites spread out in the molecular layer. Their axones pass along several Purkinje cells and end in basket-like branches about them. They are especially thick in birds. They bind the Purkinje cells together into small groups and in addition probably represent another excitation circuit through the cerebellum since their baskets appear to end close about the bodies and axone hillocks of the Purkinje cells. Other small cells of the stellate type (*s*) shown in figure 154 also are found in the cerebellar cortex.

Each Purkinje cell (fig. 156) emits a single stout axone which soon becomes covered with a myelin sheath. It penetrates the granular layer (*G*) and enters the medullary substance (*F*) and terminates in bush-like arborizations around the cells of the dentate nucleus (*nd*), or the fastigial nucleus (*fas*). Injuries to the cerebellar cortex produce abundant degenerations of these Purkinje axones into the cerebellar nuclei; whereas injuries of these nuclei produce a degeneration of the uncinate fasciculus (*uf*) and the brachium conjunctivum (*bc*).

The Purkinje fiber (*a*) as it is passing through the granular layer gives off two or more **collaterals** (*k*) that pass back and arborize around the neighboring Purkinje cells. These "backfire" collaterals (*k*) appear to be another means of providing for spread and unison of discharge among neighboring Purkinje cells.

Association bundles have not been convincingly demonstrated in the cerebellum. It would seem that irradiation must be a local phenomenon in the cerebellar cortex, depending for its extent on the distribution of incoming fibers (*cli*, *moss*), the granule cells (*g*), basket cells (*b*) and the backfire collaterals (*k*).

The **dentate nucleus** (*nd*) is a wrinkled lamina of nerve cells in the core of the white matter of each cerebellar hemisphere (figs. 143, 146, 147). On its lateral side it is enclosed by the brachium pontis (*bp*) and restiform body (*rb*). Fibers (*a*) from the Purkinje cells enter it from all sides, most abundantly from the lateral lobes, (*ans*) and end in bush-like arborizations around its cells (fig. 156). The cells of the dentate nucleus and fastigial, emboliform and globossal, are stellate with spiny branching dendrites. They are embedded in the bush-like arborizations of the axones of the Purkinje cells. They give off axones that enter the brachium conjunctivum (*bc*) which is formed on the medial side of the nucleus (fig. 152). The brachium passes cephalad into the recticular formation of the midbrain where it turns ventrally to the midline and decussates with its fellow of the opposite side (*bcx*). In the decussation, the fibers bifurcate into descending and ascending fibers. The descending fibers form the descending limb of the brachium conjunctivum (*dbc*) seen on each side of the midline terminating in the **ventral tegmental nucleus** (*nrB*). The ascending fibers pass up ending largely in the **red nucleus** (*rn*) in dense pericellular networks. Some pass beyond the red nucleus and end in the medial part of the reticular subthalamic nucleus (*sub*). The large multipolar cells of the red nucleus are embedded in the dense pericellular networks of the brachium conjunctivum. They give rise to fibers that at once cross to the opposite side and form the descending **rubrospinal tract** (*rs*).

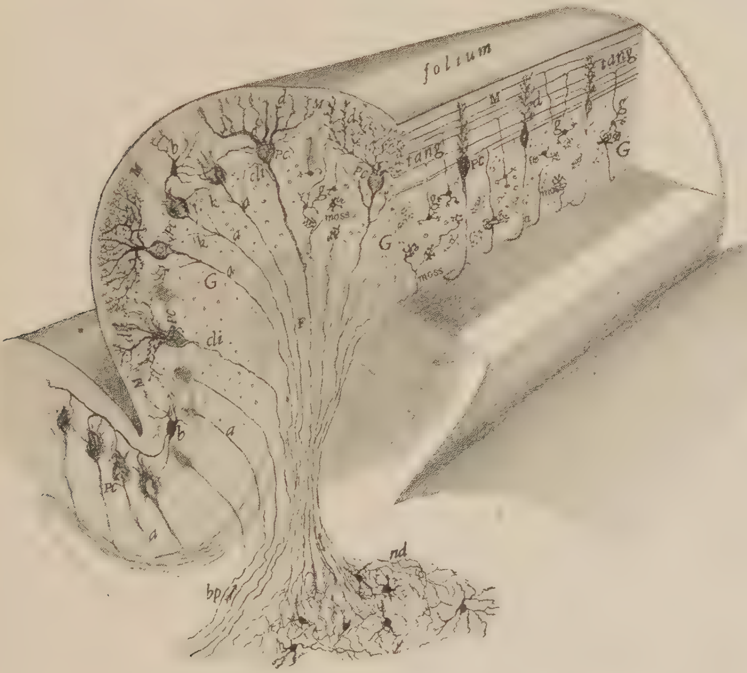

FIG. 156. Schema of cell connections in the cerebellar cortex.

Theory of cerebellar function

It seems likely from the work of Magnus that in the simple reflex adjustments of posture, the cerebellar cortex is not necessarily involved. The reflex poses of the body, limbs, head and eyes, as well as the righting and vestibular (labyrinthine) reflexes, have complete arcs of their own quite independent of the cerebellum. Thus the spinal and neck reflexes through the fasciculi proprii, the vestibular reflexes through the vestibular tracts and the optic reflexes through the tectospinal tracts can be evoked without calling into action the cerebellar cortex. From the plans of the cerebellar connections (figs. 150, 152) it will be seen that its cortex and nuclei are nowhere directly connected with nuclei of motor nerves. Luciani has shown that a loss of the tonic functions of the cerebellum can be sufficiently compensated for by the motor regions of the cerebrum; but that reflex tonus is never in itself adequate for the purpose. From its anatomical connections, and from the work of Luciani and of Magnus, it is fair to assume that the cerebellum has no direct or independent motor function, but that its tonic influence is exercised upon the various reflex mechanisms with which it is in connection.

The cerebellum deals exclusively with the motor functions, including postures and coördinated movements. Its cortex may be considered to be a dynamic motor field designed to maintain or alter the rate of flow of excitor impulses into the muscles. It not only reinforces reflex tonus (inherent in the muscular and vestibular arcs) but also subconsciously helps to maintain all manner of postures (postural tonus) imposed upon the muscles and provides for the precise regulation of the duration, strength and speed of muscular movement. These are important synergic functions.

Plans of the two chief cerebellar connections are represented in figures 150 and 152. It is seen that the cerebellar cortex receives impulses from two general sources. There are likewise two efferent systems of centers and fiber tracts that discharge cerebellar impulses into the lower motor centers.

A plan of the first or vermian system is shown in figure 150. From the lower receptive (sensor) centers the restiform body (*rb*) discharges into the vermis. These are chiefly proprioceptive impulses from the muscles and joints coming in by way of the spinocerebellar tracts (*dsc, vsc*), though tactile impulses probably come in through the laterocerebellar fibers (*lc*). The nature of the impulses from the accessory olives (*von*) is not understood but they are probably proprioceptive and deal with reflex adjustments of the head and neck. The Purkinje cells discharge into the fastigial nuclei (*fas*) and these by the uncinate bundle (*uf*) into the vestibular nuclei (*lvn, dvn, svn, mvn*), which in turn discharge through the vestibular tracts (*vs, cvs, vm, cvm*) into the lower motor centers. The result is extensor, antigravity and postural tonus of an exaggerated kind.

The action of this mechanism becomes evident in a decerebrate animal in which the mid-brain is cut through so as to sever not only the cerebral peduncles (*cp*) but also the rubrospinal (*rs*) and striatal connections. The " decerebrate " or extensor rigidity which ensues is a persistent motionless antigravity or postural tonus which depends upon a tonic reflex circuit through the cerebellum freed from the opposing influence of the cerebral cortex and red nucleus. This rigidity appears to be a function of the vermis discharged through the uncinate fasciculus (*uf*) and vestibular tracts, for it is abolished when these efferent tracts or when the afferent spinocerebellar connections are cut. For further details see chapter 24.

A plan of the second system is shown in figure 152. It concerns chiefly the lateral lobes (the ansiform and paramedian lobules). The cerebral cortex discharges impulses through the cerebropontal tracts (*cpo*) and brachia pontis (*bp*) into the lateral lobes and probably also into the vermis. The reticulocerebellar fibers (*rc*) also discharge into the lateral lobes, particularly into the large paraflocculus (*pfl*) of lower mammals. The optic tectum through the tegmental nucleus (*teg*) and the tecto-olivary tract (*to*) discharges into the olivary sac (*os*) and this in turn through the olivo-cerebellar fibers (*oc*) into the lateral lobes. The lateral lobes (*ans*) on the other hand discharge into the dentate nuclei (*nd*) and these by the brachia conjunctiva (*bc*) into the red nuclei (*rn*), which in turn discharge through the rubrospinal tracts (*rs*) into the lower motor centers.

In the mammals the cerebrum acquires a progressively increasing control over the cerebellar function through the development of the cerebro-ponto-cerebellar connections, and the large lateral lobes of the cerebellum.

The functions and connections (fig. 152) of the lateral lobes are thus complicated by the cerebral as well as striatal connections. It is believed that the excitations that come down through the cerebropontal (*cpo*) and ponto-cerebellar (*bp*) tracts can either inhibit or excite the tonic activity of the cerebellar cortex; and thus control the nature, strength, speed and duration of any voluntary movement.

In a decerebrate animal, such as the Goltz dog, the cerebral cortex has been removed and with it the cerebro-pontal and cerebrospinal tracts. In such an animal the brachia conjunctiva and rubrospinal tracts and their connections with the striate body through the subthalamus are intact, and the excitations of the lateral lobes of the cerebellum may thus reach the lower motor centers and the muscles through these connections. Such animals are capable of coördinate movements in spite of an increased tonus of their muscles. This has led to the view that the lateral lobes of the cerebellum regulate the tonus of movement. This may be thought of as a rapid alteration of posture. Such animals also show that some of the essential coördinated movements like the righting reflexes and locomotion can be performed by the lower reflex arcs in connection with this cerebellar circuit without the aid of the cerebrum.

We may assume that the real function of the cerebro-ponto-cerebellar connections is to enable the cerebral cortex to modify and adapt these essential coördinated movements to the changing needs of the animal. In this way the dynamic functions of the cerebellum come to be controlled and trained under the selective guidance of the cerebral cortex, leading to the adaptative responses. This adaptative function is the most characteristic feature of cerebral activity or animal intelligence (see Chapter 33). In its motor responses it calls into action the circuits through the cerebellar cortex in which inhibition and excitation are nicely graded and distributed to the appropriate muscle groups.

Functional subdivisions of the cerebellum

The principles of coördination, integration and tonus of muscular activity prevail in the arrangement of the spinal reflex arcs, cerebellar circuits and cerebro-cerebellar and spinal circuits. In other words, coördination is inherent in the organization of the entire motor system. Accordingly, it is natural to find that the various areas or lobes of the cerebellar cortex stand in supposed categorical relations with the various functional muscle groups and flexion areas of the body, by means of afferent and efferent fiber systems.

From comparative studies Bolk has presented the view that the several lobules of the cerebellum stand in connection with particular functional groups of muscles. The subdivisions of Bolk and Ingvar are along natural lines and correspond to the morphological subdivisions as they have been worked out by Smith and others (see Chapter 10).

According to the view of Bolk the median unpaired portions of the cerebellum that form the vermis are centers for the bilateral head and trunk muscles that function together. The **anterior lobe** in front of the fissura prima (*fp*) is in connection with the reflex and cerebral mechanisms that control the muscular movements of the eyes, jaws, face, tongue, pharynx and larynx. The **lunate lobule** (*lun*) just back of the fissura prima is in connection with the cervical tracts which serve to control the movements of the head and neck. The **tuber vermis** is concerned with bilateral movements of the extremities. The **pyramis, uvula** and **nodulus** are concerned with movements of the trunk. The **lateral lobes** are concerned with movements of the limbs; most of the **ansiform lobule** (superior and inferior semilunar lobules) is concerned with movements of the fore-limb. The posterior part of the ansiform lobule (biventral) and probably also the **paramedian lobule** (tonsil) are concerned with the movements of the lower limb. The degree of development of these lateral cerebellar lobes in the different vertebrates is also correlated with that of the pons and cerebral cortex. They attain great proportions in the Primates. The paraflocculus is greatly reduced in the three tailless anthropoid apes and man. The animal experimentations of Van Rynberk and others appear in the main to support the views of Bolk.

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CHAPTER 27

The Cochlear System

The **cochlear centers** and tracts should now be followed out on the sections (from fig. 141 to fig. 166). It begins with the cochlear nerve (*nc*) and nuclei (*vcn, at*) in the upper oblongata and extends upwards through the pons, isthmus and midbrain as the lateral lemniscus (*tb, ll*) to reach the medial geniculate body (*mg*). From the medial geniculate body the auditory radiations (*ar*) extend to the temporal cortex. In the lower mammals most of this conduction system can be followed on the outer surface of the brain stem (see page 124). It conducts auditory impulses from the cochlea to the temporal region of the cerebral cortex where the function of hearing is effected.

The **bony cochlea** is a coiled, snail-like formation of the petrosal bone medial to the promontory which encloses the **spiral canal of the cochlea** (fig. 157). The cochlea is placed horizontally. Its base faces backwards in the anterior wall of the bottom of the internal acoustic meatus through which it is entered by the cochlear nerve (*nc*). Its apex points forwards against the carotid canal and auditory tube. The promontory (*prom*) covers the lateral surface of the large basal coil of the cochlea. The spiral bony canal is wound two and three-quarters times around a central screw-like axis, the **modiolus.** It is divided into a large basal turn, an intermediate middle turn and a small apical turn. The basal turn commences in the promontory, passes medially below the modiolus and then upwards and laterally around the modiolus into the middle turn. The middle and apical turns describe a similar course. The turns are completely separated from one another by a spiral septum of bone (*zw*) which stretches from the modiolus to the lateral wall of the cochlea. In addition, a bony **spiral lamina** (*lspo*) projecting from the modiolus partially separates the bony canal into an anterior portion, the **vestibular canal** (*scv*) and a posterior portion, the **tympanic canal** (*scty*). At the apex the spiral lamina terminates incompletely so that the two canals communicate with each other. In the basal coil (*prom*) there is a slight **secondary spiral lamina** in the lateral wall opposite the spiral lamina. The **modiolus** has a broad base that faces into the bottom of the internal acoustic meatus and is perforated by numerous foramina which constitute the **tractus spiralis foraminosus** for the exit of the cochlear nerve (*nc*). These foramina lead into numerous channels in the modiolus and the spiral lamina (*lspo*) which lodge the nerve filaments and spiral ganglion (*ggsp*), the cells of which give origin to the cochlear nerve (*nc*).

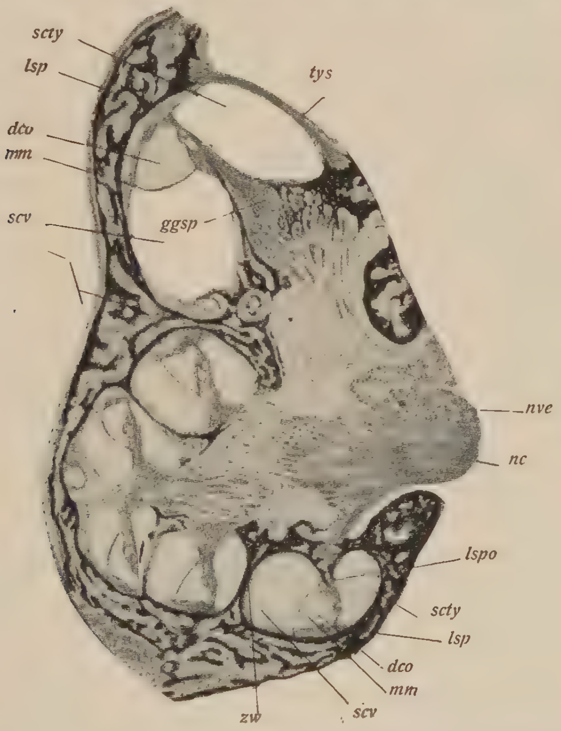

Fig. 157. Section of cochlea of young cat. After Krause.

Examine a section of the cochlea (fig. 157) of a cat and make out the following details. The bony cochlea contains the narrow membraneous cochlear duct (*dco*), which contains the long organ of Corti. The spiral canal of the **cochlea** is only partly occupied by the smaller membranous **cochlear duct** (*dco*). This is placed between the outer margin of the spiral lamina (*lspo*) and lateral wall of the cochlea on the anterior surface of the thick spiral ligament (*llsp*). In this way the bony spiral canal is completely subdivided into an anterior tube, the **vestibular canal** (*scv*), and a posterior tube, the **tympanic canal** (*scty*). The cochlear duct (*dco*) is everywhere interposed between the two canals except at the apex of the cochlea where the canals communicate with each other (helicotrema). The canals are lined with a thin periosteal membrane and are filled with a fluid, the **perilymph.** The relation of the canals to the cochlear duct is of great functional importance. The vestibular canal begins in the basal coil of the cochlea near the foot plate of the stapes, at which waves in the perilymph commence when the stapes vibrates. The canal and also the fluid vibrations proceed towards the apex in front of the spiral lamina and the thin **vestibular membrane** (*mm*) that forms the posterior wall of the scala vestibuli (*scv*) and the anterior wall of the cochlear duct (*dco*). It is the vibration of this membrane that is transmitted to the tectorial membrane (*mte*) which in turn stimulates the organ of Corti. At the apex (helicotrema) the vestibular canal passes into the tympanic canal; and a like course is taken by the vibration. The tympanic canal (*scty*) commences at the apex and proceeds to the base behind the spiral lamina (*llsp*) and the basal membrane (*mba*). It ends blindly at the secondary **tympanic membrane** (*tys*) which stretches over the fenestra cochleae. The basal membrane (*mba*) which separates the tympanic canal from the cochlear duct is thick and covered on its posterior surface by vascular connective tissue. Throughout, both of the canals are lined by a thin endothelial membrane.

The **cochlear duct** (fig. 158, *dco*) is a narrow membranous channel containing the **spiral organ** of Corti (*stz*) and jelly-like fluid, the **endolymph.** It is attached between the spiral lamina of the modiolus (*llsp*) and the lateral wall of the cochlea where it lies on the front surface of the spiral ligament (*mbc*) describing two and a half turns. It separates the vestibular canal from the tympanic canal except at the apex (helicotrema). In transverse section it is triangular. The anterior wall is formed by the thin **vestibular membrane** (*mm*). This separates the perilymph of the vestibular canal from the endolymph of the cochlear duct, but its thinness allows the waves in the perilymph to affect the endolymph. The outer wall is formed by the **spiral ligament** (*lsp*), a thickened inner periosteum. This is lined by a thick vascular epithelium. The posterior wall is formed by the basal membrane (*mba*) and in part by the spiral lamina of the modiolus. The basal membrane stretches from the margin of the spiral lamina to the spiral ligament. It is a thick fibrous structure and upon its anterior surface is placed the spiral organ (of Corti). Stretching from the spiral lamina in front of the spiral organ is the **tectorial membrane** (*mte*).

The **spiral organ** of Corti (*stz*) is the essential end organ of hearing containing the auditory hair cells which are connected with the peripheral processes (dendrites) of the auditory nerve (*nc*). The organ forms a spiral ridge of epithelial cells placed upon the anterior surface of the basal membrane within the cochlear duct. It consists of: (1) two rows of supporting **rods of Corti** (*ipf*, *aepf*) which are braced against each other over the tunnel of Corti, (2) an inner and outer set of **hair cells**, (3) **supporting cells** (*stz*) which support the hair cells, (4) cells of Hensen (*hw*) and (5) cells of Claudius (*zcl*). The inner set of hair cells (*ihz*) is formed by a single row (3500), and the outer set is formed by three rows (12,000).

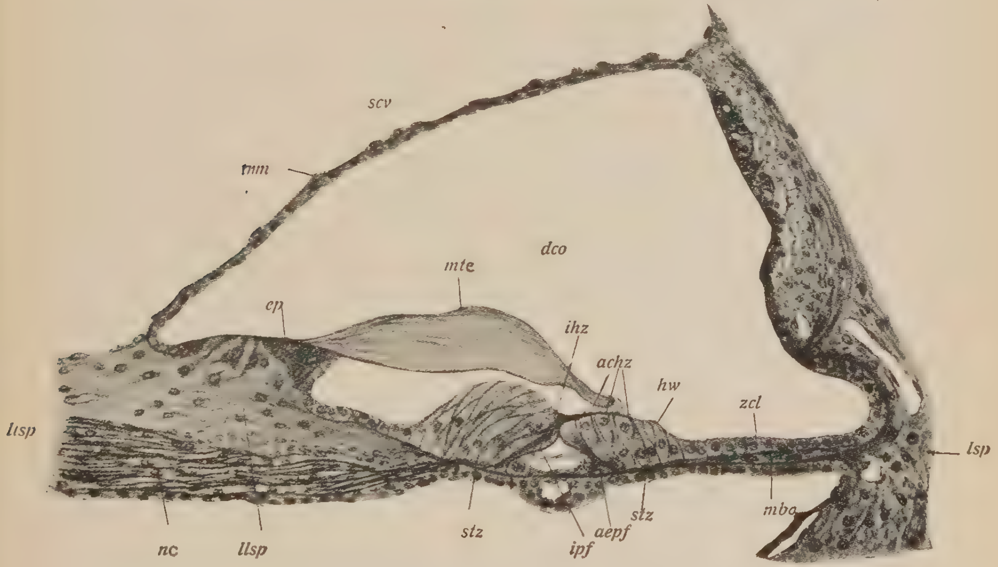

Fig. 158. Section of cochlear duct and organ of Corti of a cat. After Krause.

From the structure of the cochlea the following **theory of audition** may be formulated. The vibrations of the foot plate of the stapes are transmitted to the perilymph of the vestibular canal along which they are propagated to the helicotrema where they enter the tympanic canal. The vestibular membrane is thin and it is believed that it transmits the waves in the perilymph of the vestibular canal (*vsc*) to the endolymph in the cochlear duct (*dco*), which through the action of the tectorial membrane (*mte*) stimulates the hair cells of the spiral organ. From the helicotrema the waves in the perilymph retrace their course along the tympanic canal (*scty*) to the fenestra cochleae (*tys*). The spiral organ probably is not stimulated by these waves in the tympanic canal. Waves in the endolymph coming from the vestibular membrane are believed to make the tectorial membrane (*mte*) undulate against the hair cells of the spiral organ of Corti and in this way act as auditory stimuli. Thus every simple sound that vibrates the stapes would be propagated through the whole length of the vestibular canal and cochlear duct and would distribute, by means of the undulating tectorial membrane, a **succession of stimuli along the whole length of the organ of Corti.** High pitch would make more frequent contacts on the organ than low pitch before the wave reaches the helicotrema. Every pitch, tone and sound, of whatever combination of tones, would of necessity be a succession of stimuli, each element being conducted over the entire length of the organ of Corti which it stimulates at a large number of points. An essential factor for this type of wave propagation would be the elastic nature of the endolymph which would be responsible for the wave-like effect on the organ of Corti.

The **cochlear nerve** (*nc*) connects the hair cells of the spiral organ with the cochlear nuclei of the oblongata. It is derived from the cells of the **spiral ganglion** (*ggsp*) which is located in the canal of the modiolus along the base of the spiral lamina. From the spiral ganglion numerous (4000) dendritic filaments (*nc*) pass outwards through foramina in the spiral lamina to the hair cells of the spiral organ. The root filaments from the spiral ganglion pass through the channels in the modiolus and enter the internal acoustic meatus through the **tractus spiralis foraminosus.** In the internal acoustic meatus they accumulate to form the auditory nerve (*nc*). The nerve lies at first in front and as it comes to the oblongata somewhat dorsal the vestibular, facial and glossopalatine nerves.

The cochlear nerve crosses the lateral medullary cisterna of the arachnoid and terminates in the two cochlear nuclei (*at*, *vcn*) situated dorsal and ventral to the restiform body (*rb*). In sections (figs. 142–147) of the stem the stump of the cochlear nerve may be seen, but it is usually torn out of the acoustic tubercle (*at*). The **dorsal cochlear nucleus** or **acoustic tubercle** (*at*) is curved over the dorsolateral surface of the restiform body (*rb*). It is rudimentary in the human brain. The large **ventral cochlear nucleus** (*vcn*) is seen in its ventral end. The cells of the acoustic tubercle are small. They are said to receive some of the terminals of the cochlear nerve. The fibers seen in this nucleus are the **acoustic stria** (*as*). The stria arise (figs. 141–143) from the cells of the acoustic tubercle (*at*), cross over the restiform body (*rb*), pass through and penetrate the vestibular nuclei (fig. 143).

No distinct cochlear stria are to be seen in the surface of the floor of the fourth ventricle as in the human brain. Examine the floor of the fourth ventricle in several (demonstration) human oblongatae, to get an idea how variable these stria are. In lower animals they never appear on the surface. In human sections the stria are interrupted by the small nuclei teretis near the midline. From this point the stria pass ventrally in the raphe and soon cut through the tectospinal tract and reticular formation to reach forward to the superior olive of the other side. In this part of their course they cannot be readily followed since they are dispersed in the reticular formation. Dorsal to the superior olive they form a distinct tract which overcaps the two segments of the olive. It is probable that they make a functional connection with the lateral superior olive. There is a close resemblance in cell structure between the acoustic tubercle and the superior olive.

As shown in figure 159 the acoustic stria (*as*) in the cat arise from the acoustic tubercle (*at*) ; as a compact bundle they penetrate the vestibular nuclei (fig. 143) and spray out in the center of the reticular formation. Here they divide, one half going to the lateral *S*-shaped segment of the superior olive (*so*) on the same side, and the other half crossing to the midline and to the lateral *S*-shaped segment of the superior olive of the other side. Dorsal to the olives they turn upwards and pass without interruption to the inferior colliculus. They form the medial division of the lateral lemniscus (figs. 147, 151, 161, 162, *as*).

The **ventral cochlear nucleus** (*vcn*) is seen on the lateral side (figs. 141 to 151) lateral to the restiform body (*rb*). In the human brain two parts are recognized, a medial and a lateral. Traced up, they become separated by the incoming vestibular root. The ventral cochlear nucleus is large, contains large nerve cells and is closely connected with the acoustic tubercle (*at*). It receives a large part of the cochlear nerve root, the terminals of which give it a very dark appearance. Notice that its lateral surface is covered by the lighter acoustic tubercle (*at*). These cochlear nuclei give origin to the fibers that pass over the dorsal surface of the restiform body and go to form the acoustic stria (*as*).

The **trapezoid body** (*tb*) or crossing of the lateral lemniscus is a large band of fibers that arise from the ventral cochlear nucleus (*vcn*) on each side. It appears as a thick band of fibers coming from the medial side of these nuclei and passing ventrally over the surface of the descending root of the trigeminus and the superior olive (figs. 143–151). Into the superior olive it sends a large group of collaterals. Passing ventral to the olives the trapezoid body passes through the medial lemniscus (*ml*) and decussates with its fellow of the opposite side (figs. 146–151). In the brains of lower animals the trapezoid body is seen on the ventral surface caudal to the pons (figs. 73, 74). In the human brain it is completely covered by the backward over-growth of the pons. The large fiber tract in its decussation is the **medial lemniscus** (*ml*) going upward. The fiber tract medial to the superior olive is the **tecto-olivary tract** (*to*). The small tract over the dorsal surface of the olive is the **acoustic stria** (*as*). Around the ventral side of the superior olive the fibers of the lateral lemniscus (*ll*) turn forward and form a crescentic bundle, which at first is hard to separate from the medial lemniscus (*ml*) on its medial side and from the rubrospinal (*rs*) and the ventral spinocerebellar (*vsc*) tracts on the lateral side. Followed upward it (*ll*) surrounds the superior olive.

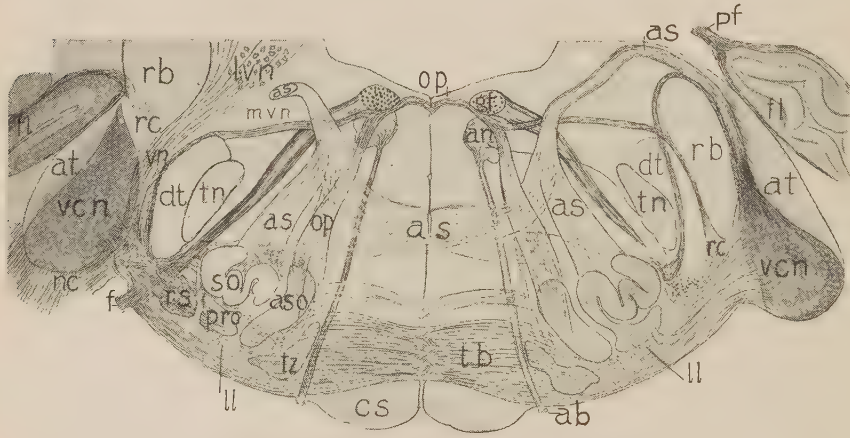

FIG. 159. A diagrammatic section of the origin of the acoustic tracts in the cat.

The **superior olive** consists of the lateral *S*-shaped segment (*so*), medial accessory segment (*aso*) and nucleus of the trapezoid body (*tz*). A small preolivary nucleus (*pro*) is found ventral to the lateral segment (*so*). At higher levels it (*pro*) is replaced by the nucleus of the lateral lemniscus (*nll*). In the human brain it is the lateral segment (*so*) that is very small (rudimentary) but in the cat it is highly developed.

The **cells in the superior olive** are fusiform, bipolar elements that resemble closely those in the acoustic tubercle (*at*). They are embedded in the elongated brush-like terminals from the trapezoid body (*tb*). Their axones pass into the lateral lemniscus (*ll*). The term lateral lemniscus is applied to the fiber system that extends from the superior olive to the inferior colliculus (*ic*). It consists of, (1) trapezoid fibers, (2) acoustic stria and (3) fibers from the superior olive. From the medial segment (*aso*) or from the trapezoid nucleus (*tz*) there arises a tract of fibers, the **olivary peduncle** (*op*), that passes dorsally through the abducens nucleus (*an*), crosses the midline beneath the facial genua (*gf*) and passes out over the trigeminal root (*dt*) to reach the ventral cochlear nucleus (*von*). Beyond this point its course is not known.

Above the level of the superior olive (fig. 161) the lateral lemniscus acquires in its core, the **nucleus of the lateral lemniscus** (*nll*). In the same sections the ventral spino-cerebellar tract (*vsc*) is seen to turn dorsally over the external surface of the lateral lemniscus and the brachium conjunctivum. The rubrospinal tract (*rs*) is now dorsal to the lateral lemniscus. In this region the lateral lemniscus is beginning to turn dorsally to pass over the side of the brachium conjunctivum as these brachia are shifting ventrally. Traced up, the lateral lemniscus (*ll*) is seen to enter the inferior colliculus (figs. 162 and 163). The **nucleus of the lateral lemniscus** (*nll*) here gives rise to the commissural fibers (*cll*) of the same name, which pass medially over the brachium conjunctivum (*bc*) toward the central gray. Here the commissural fibers (*cll*) decussate and by the same route enter the inferior colliculus (*ic*) of the other side. Besides the commissure of the lateral lemniscus (*cll*) another fiber tract, the **central acoustic tract** (*cat*) emerges from the nucleus of the lateral lemniscus just where this enters the inferior colliculus. This tract passes directly forward to the medial geniculate body and, as Cajal has shown, contributes collaterals to the inferior colliculus.

The **inferior colliculus** (fig. 163, *ic*) is a solid oval mass of cells in which the large bundles of the lateral lemniscus terminate. Fibers that reach the inferior colliculus are arranged in separate systems:

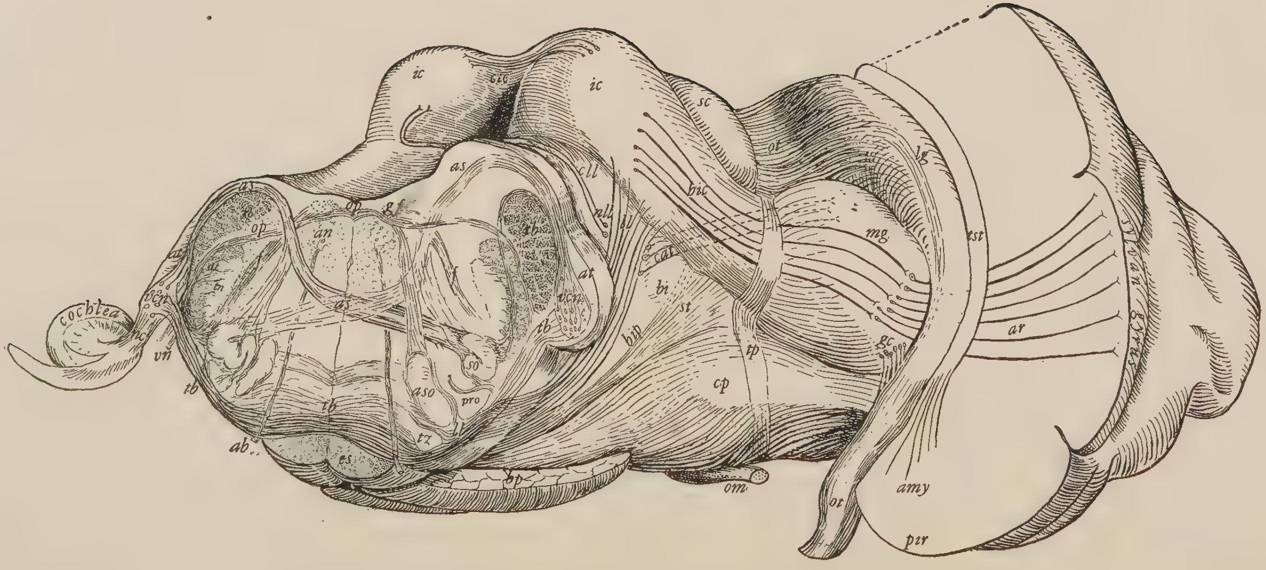

FIG. 160. Diagram of the acoustic paths in the brain stem of a cat.

(1) the acoustic striae (*as*) direct from the acoustic tubercle, (2) the trapezoid fibers (*tb*) from the ventral cochlear nuclei, (3) fibers of the nuclei of the lateral lemnisci, (4) fibers of the commissure of the lateral lemniscus (*cll*), (5) fibers from the superior olive and (6) fibers from the inferior colliculus of the other side (*cic*).

The inferior colliculus and superior olive form essential links in the auditory conduction system, to which they both contribute ascending fibers. Reflex functions have often been ascribed to them; but definite reflex tracts from them to motor centers have not been established.

The functions of the parabigeminal nucleus (*bi*) and the bigeminopontal tract (*bip*) are unknown. It seems probable that these structures correspond to the semilunar nucleus (*semi*) and the tract (*bip*) of Birds (fig. 246, p. 421) and homologous structures in Fishes.

Fibers from the inferior colliculus (fig. 160) pass forward on the lateral surface of the mid-brain forming the **brachium of the inferior colliculus** (fig. 165, *bic*). They terminate by arborizing among the cells of the medial geniculate body (fig. 166, *mg*). Medial to the brachium is the **central acoustic tract** (*cat*) which consists of much finer fibers from the nucleus of the lateral lemniscus. The central acoustic tract (*cat*) as well as the brachium (*bic*) end in the medial surface of the **medial geniculate body** (fig. 166, *mg*). This (*mg*) appears as a large superficial gray mass. On its outer surface a thin stratum of fibers appears, the **geniculate commissure** of Gudden (*gc*) which joins the optic tracts and along them passes around the ventral surface of the thalamus to end in the medial geniculate of the other side.

The **medial geniculate body** (*mg*) is a large mass of stellate and bipolar cells around which the fibers of the brachium (*bic*) and central acoustic tract (*cat*) end. These cells give off axones that pass medially and anteriorly and form the large **auditory thalamo-cortical radiations** (*ar*). These soon replace the brachium and central acoustic path and turn laterally to enter the internal capsule medial to the **optic radiations.** These auditory radiations pass in the posterior limb of the internal capsule anterior to the point where the middle part of the lateral ventricle joins the ventral horn of the ventricle. They terminate in the cortex of the **anterior transverse temporal gyrus** of Heschl in the human brain. This is the **auditory area** of the cerebral cortex. In the brain stem (fig. 160) locate the lateral lemniscus (*ll*), the inferior colliculus (*ic*), the brachium of the inferior colliculus (*bic*) and the medial geniculate body (*mg*). On the cortex locate the auditory area, and determine what course the auditory radiations (*ar*) from the medial geniculate body must take to reach this area. In the Carnivora the sylvian gyri represent the auditory area while the ectosylvian and suprasylvian probably form an extensive auditory cortical analyser. Through the corpus callosum (*cc*) the auditory areas are connected with each other. Experiments have shown that even in the dog the left side dominates as a functional analyzer. The trapezoid (*tb*) and strial (*as*) decussations of the auditory paths in the oblongata, the collicular (*cic*) and lemniscal (*cll*) commissures in the midbrain and the geniculate commissure (*gc*) at the thalamic level make it certain that auditory impulses from both ears pass up on both sides and reach both auditory areas.

As has been pointed out, the auditory pathway is formed of several streams of fibers that have different synaptic arrangements; in addition they vary among themselves in number of neurones, length and caliber of fibers. It is evident that the auditory impulses delivered into the cortex by these different streams cannot be of uniform pulse. It is possible that these several subcortical streams provide some basic subcortical element in sound analysis such as musical interval.

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CHAPTER 28

STRUCTURE OF THE MIDBRAIN

Sections through the Inferior Colliculus

A SECTION (fig. 161) through the isthmus cuts across the pontal protuberance (*pp*). Its three constituent parts are easily recognized: (1) the **cerebral peduncles** (*cs, cpo*) surrounded by the (2) **pontal nuclei** (*pn*) in which the cerebropontal tracts (*cpo*) end, (3) the **pontal fibers** which arise within the nuclei, cross and condense laterally to form the **brachia pontis** (*bp*) which enter the cerebellar cortex. The cerebropontal (*cpo*) and pontocerebellar system (*bp*) discharges cerebral impulses into the cerebellar cortex (fig. 152). The cerebrospinal tracts (fig. 151 *cs*) which form a part of the cerebral peduncles pass through the **pontal nuclei** into the oblongata and cord.

On the dorsal surface of the pontal nuclei (fig. 161) is the **medial lemniscus** (*ml*) which is passing upwards through the midbrain to reach the ventral-lateral or arcuate nucleus (*arc*) of the thalamus. On its lateral side lies the spinothalamic tract (*sth*) and **lateral lemniscus** (*ll*) enclosing the **nucleus of the lateral lemniscus** (*nll*). The acoustic stria (*as*) form the medial part of the lateral lemniscus. In their dorsal part the **rubrospinal tract** (*rs*) appears as a dense fiber tract: it is coming down from the red nucleus of the other side. The ventral spinocerebellar tract (*vsc*) curves dorsally over the surface under cover of the brachium pontis (*bp*).

The **brachium conjunctivum** (*bc*) is sinking ventrally into the reticular formation on its way upward to the red nucleus of the other side. Over its outer surface the ventral **spinocerebellar tract** (*vsc*) is looping dorsally to reach the anterior lobe (chap. 10, *la*) of the cerebellar cortex. On the medial side of the brachium (*bc*) are seen scattered bundles of fibers that appear to enter the anterior side of the masticator nucleus (*mn*). They appear to come out of the brachium or gray mass that surrounds it. The **mesencephalic root of the trigeminus** (*mes*) is medial to the brachium. Ventral to this root is the **locus caeruleus** (*loc*), from which the tract of Probst (*Pt*) appears to take origin.

In the center of the **reticular formation** is the **central tegmental fasciculus** (*cf*) consisting of the trigemino-thalamic tract and the dorsal spino-thalamic tracts seen at lower levels of the oblongata. These tracts are passing up to the central and reuniens nuclei of the thalamus (fig. 170, *cnt*, *reu*). More ventrally over the medial lemniscus is the **tecto-olivary tract** (*to*) and probably also ascending gustatory tracts from the vagal nuclei (*gu*). The large cells scattered through the reticular formation form the **reticular nucleus** of the pons (*nrp*) which give rise to the **reticulo-spinal tracts** (*mrs*). Four tracts are ranged along each side of the central reticular nucleus (*nrc*) along the midline, most dorsal being the crossed **vestibulo-mesencephalic tracts** (*cvm*) that form the main part of the medial longitudinal fasciculus and the direct vestibulo-mesencephalic tracts (*vm*) that form its lateral horn. Just ventral to them is the medial reticulo-spinal tract (*mrs*). In the middle are the **tecto-spinal** (*ts*) and interstitio-spinal tracts. Ventrally over the medial lemniscus is the **descending limb of the brachium conjunctivum** (*dbc*) scattered within the **ventral reticular nucleus** (*nrB*). In the midline are the **reticulo-cerebellar fibers** (*rc*) passing ventrally from the

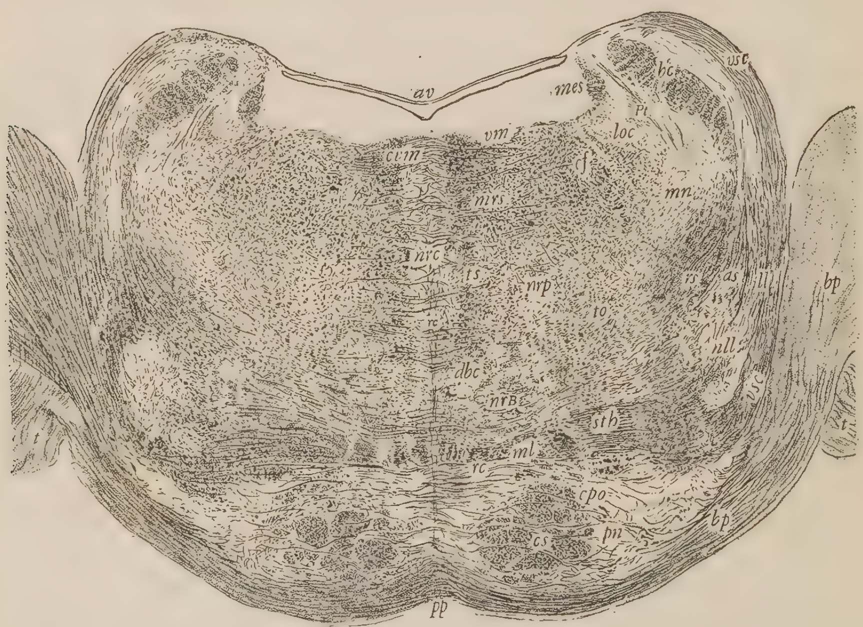

FIG. 161. Section through the isthmic region just back of the inferior colliculus, cat, × 8½.

ventral reticular nucleus into the pontile nuclei where their fibers separate to join those of the brachia pontis.

A section through the inferior colliculus (fig. 162) repeats all the foregoing features. In addition the **inferior colliculus** (*ic*) rises dorsally as a large oval mass on each side of the **cerebral aqueduct** (*aq*). This is roofed over by the thin anterior medullary velum. The **lateral lemniscus** (*ll*) is entering the ventral surface of the colliculus (*ic*) and sends great quantities of fibers into it. Fibers from the cells of the colliculus appear upon its lateral surface as the **brachium of the inferior colliculus** (*bic*) which passes forward (fig. 164) to the medial geniculate body (fig. 165, *mg*). On the surface of the lateral lemniscus (fig. 162) is a tract of fine fibers (*bip*) which passes from the bigeminal nucleus down to the lateral part of the

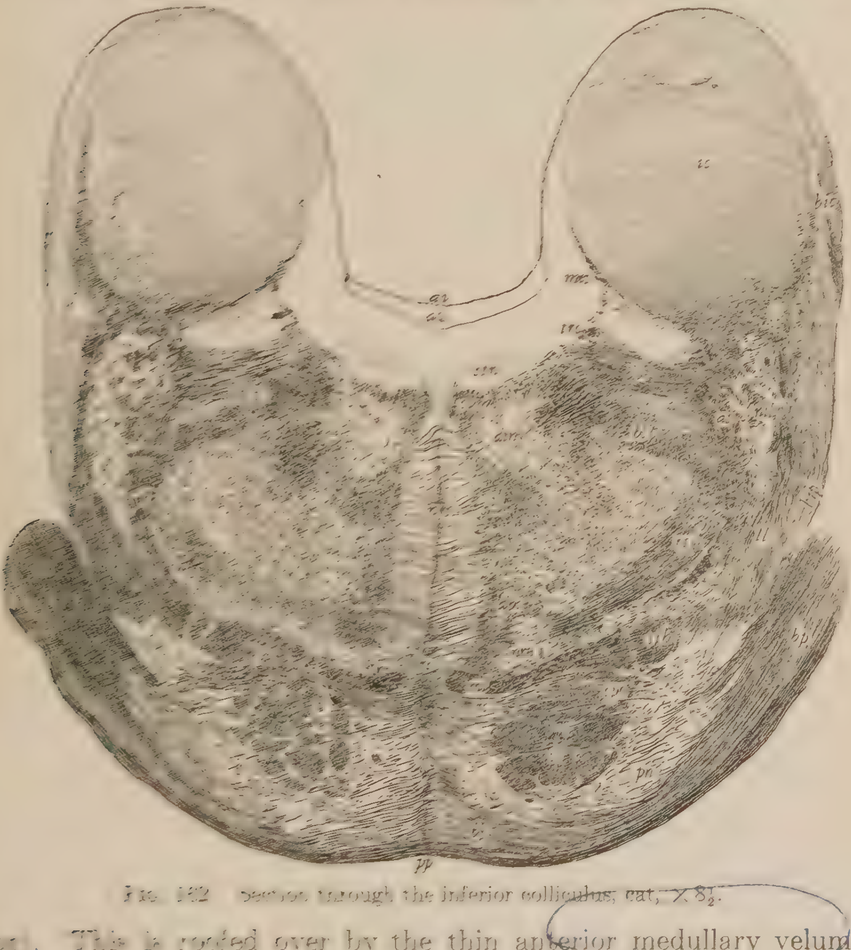

Fig. 162.—Section through the inferior colliculus; cat, × 8½.

pontal nucleus. This is an obscure connection that the collicular region makes with the cerebellum.

The **mesencephalic root of the trigeminus** (*mes*) and its globular cells are seen along the medial side of the colliculus. It is passing down to join the masticator nerve (fig. 151, *mn*). Its relations to the colliculi (fig. 162) have been explained by assuming that it is a sensory nerve whose globular cells of origin (neural crest) have been retained in the midbrain region. The **trochlear nerve** (*tro*) is seen passing down in the mesencephalic root (*mes*). The **brachium conjunctivum** (*bc*) is moving medially through the central tegmental fasciculus (*cf*). The **rubrospinal tract** (*rs*) is also shifting medially. The fibers that stream medially from the **nucleus of the lateral lemniscus** (*nll*) form the **commissure of the lateral lemniscus** (*cll*). They cross through the brachium conjunctivum (*bc*) and vestibulo-mesencephalic tracts (*vm*, *cvm*), intercross in the midline and by the same route reach the inferior colliculus of the other side.

The **deep tegmental nucleus** of Gudden (*dtn*) is seen just ventral to the vestibular mesencephalic tracts. In the central gray is the **dorsal tegmental nucleus** (*stn*) which receives from the interpeduncular nucleus (fig. 163, *ip*) a tract of fibers that is seen passing dorsally along the raphe. From the dorsal tegmental nucleus (*stn*) fibers pass through the tracts into the deep tegmental nucleus (*dtn*), from which in turn fibers are described as entering the reticular formation to descend with the reticulo-spinal tracts (*mrs*). The meaning of this system is obscure, though the olfacto-habenular and habenulo-interpeduncular connections make it likely that the system deals with some subcortical reactions arising in the olfactory brain. It is an ancient system prominent in the lower vertebrates.

A section (fig. 163) through the upper level of the inferior colliculi passes through the thick **collicular commissure** (*cic*) which unites them dorsal to the aqueduct (*aq*) and central gray (*cg*). On the lateral surface of the inferior colliculus the **collicular brachium** (*bic*) is growing larger. Ventral to it is the small **bigeminal body** (*bi*) which sends a band of fibers (*bip*) over the surface to enter the lateral nucleus of the pons. The bigeminal body (*bi*) may be regarded as an outlying part of the inferior colliculus which connects with the pons and through this discharges into the cerebellum. It provides a possible sub-cortical path for acoustic motor responses.

At this level the nucleus of the lateral lemniscus has dropped out but it is replaced by the **central acoustic tract** (*cat*) which passes from this nucleus forward under the colliculus to reach the medial geniculate body. The **brachia conjunctiva** (*bc*) have passed medially and are intercrossing (*bcx*) in the midline. The **tectospinal tracts** (*ts*) are seen in each side of the decussation. The **rubrospinal tracts** (*rs*) are also shifting medially with the brachium conjunctivum.

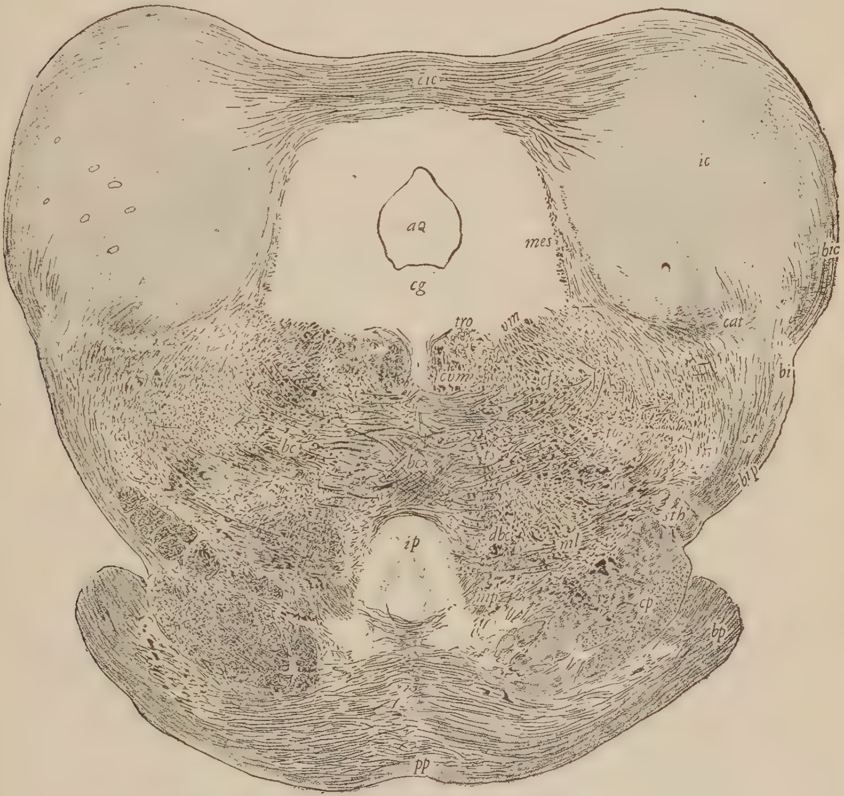

FIG. 163. Section through the inferior colliculus, cat, × 7½.

The **trochlear nucleus** (*tro*) is seen near the midline embedded in the vestibular mesencephalic tracts (*cvm*, *vm*) which send fibers into it. The **interpeduncular nucleus** (*ip*) appears as a clear mass ventral to the conjunctival decussation. Lateral to the nucleus is a dense tract, the **descending limb of the brachium conjunctivum** (*dbc*) which arises as a bifurcation of the conjunctival fibers and passes down to the ventral reticular nucleus (*nrB*) seen in the lower sections. The pontal protuberance (*pp*) is nearly gone. The medial lemniscus (*ml*) has shifted laterally and its lateral border, formed by the **spinotectal tract** (*st*), is streaming dorsalward towards the superior colliculus.

Sections through the superior colliculus

In a section across the middle of the superior colliculus (fig. 164), the **brachium of the inferior colliculus** (*bic*) forms a bulge on the lateral surface. Just medial to it is the finer **central acoustic tract** (*cat*) which in the previous sections was seen to emerge from the nucleus of the lateral lemniscus (*nll*). The **spino-tectal tract** (*st*) curves dorsally through the central acoustic tract and forms the broad middle fiber stratum of the **superior colliculus** or tectum.

The **tectum** or superior colliculus (*sc*) consists of several layers of fibers and gray matter. (1) The **superficial gray stratum** (*sgs*) forms the outer gray cap or dorsal layer. Its surface is covered by a thin layer of optic fibers, the zonal stratum. (2) Under the gray cap is a broad band of dispersed fibers; this is the **optic stratum** (*ot*) formed by the tectal or collicular division of the optic tract. (3) Deep to this is the middle gray stratum through which passes the **spino-tectal tract** (*st*). (4) Surrounding the central gray in an arch-like manner are the **tectospinal tracts** (*ts*). They arise from cells in the superficial as well as the middle gray stratum, pass radially towards the center and there curve through the **central tegmental fasciculus** (*cf*) and intercross in the midline (*tsx*) dorsal to the **red nuclei** (*rn*) and to the decussation of the **rubrospinal tracts** (*rsx*) which is seen between the two red nuclei. As they decussate the **tectospinal tracts** turn down, passing down dorsal and medial to the red nuclei and the decussation of the brachium conjunctivum. The tectospinal fibers at this level appear to send no fibers into the oculomotor nuclei but are passing down to the spinal cord. The **tecto-oculomotor fibers** that supply the ciliary and oculomotor nuclei are found only in the anterior part of the tectum (fig. 166) closely associated with the posterior commissure and interstitiospinal tracts. According to Cajal the tectospinal tracts send collateral fibers into the red nucleus (*rn*).

A large tegmental nucleus (*teg*) also called the innominate nucleus by Bechterew and lateral superior nucleus by Flechsig appears as a large clear area (fig. 164) lateral to the central tegmental fasciculus (*cf*) and red nucleus (*rn*). It is enclosed by the medial lemniscus (*ml*) on its ventral side and the spino-thalamic tract (*sth*) on its lateral side. The lateral division of the tecto-spinal tracts (*ts*) sends a great quantity of fibers into this cellular area. It also receives a large quantity of peduncular fibers from the strio-peduncular tract (*stp*). It appears to be chiefly a subtectal center. Traced downwards there is formed in it a compact tract (*to*) lateral to the central tegmental fasciculus and ventral to the inferior colliculus (fig. 163 down). At lower levels the tract (*to*) becomes lost in the brachium conjunctivum, so that its further course is not certain. One explanation is that it turns medially in the ventral border of the brachium conjunctivum and becomes the well-known thalamo-olivary tract of human anatomy. In the cat Lewandowsky has found this bundle (*to*) to arise in the tectal region and descend to the pontal level, where it turns medially around the ventral border of the brachium and descends to reach the inferior olive around the sac and dorsal nucleus in which it ends. This connection is represented in figures 152 and 166. The olivary sac is known to be connected by the olivo-cerebellar fibers with the lateral lobe of the cerebellum of the other side. It is possible that through this little known system of connections the tectum and striatum are able to excite the cerebellum and thus alter posture and direct movements by means of vision and contact.

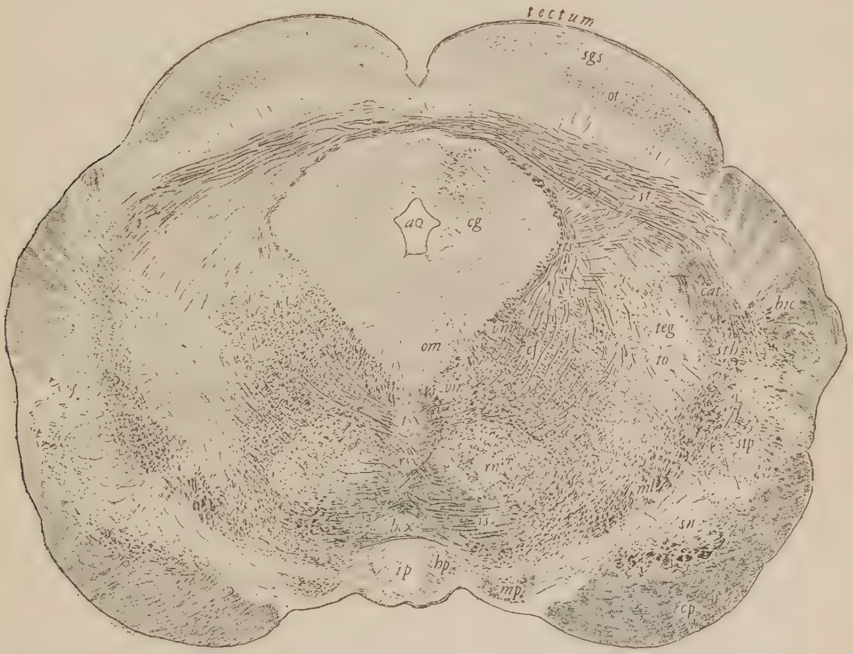

FIG. 164. Section through the middle of the superior colliculus, cat, × 7½.

The tectum or superior colliculus may be looked upon as a rudimentary optic cortex. As a result of its optic tract (*ot*) and spinotectal (*st*) connections the tectum acts as an optico-sensory reaction center which through the tecto-spinal tract (*ts*) is able to adjust the movements of the eyes, head, limbs and body. It has been shown that such reflex body directing and righting movements are exercised by the midbrain in response to visual stimuli.

The **medial lemniscus** (*ml*) forms a broad band curved around the lateral and ventral side of the great tegmental nucleus (*teg*). Its lateral part is formed by the spinothalamic tract (*sth*). Lateral to the cerebral peduncles (*cp*) is the large **strio-peduncular tract** (*stp*) which comes down from the globus pallidus. At this level it penetrates the lateral border of the medial lemniscus (*ml*) and ends in the ventral part of the tegmental nucleus (*teg*). Through these connections (fig. 152) it is probable that the globus pallidus is linked with the cerebellum, that is, through the tegmental nucleus, tecto-olivary (*to*) and olivo-cerebellar (*oc*) tracts.

The **interpeduncular nucleus** (fig. 164, *ip*) is still seen on the mid-ventral surface. On each side of it is the **habenulo-peduncular tract** (*hp*) ending in it. More lateral, also on the surface, is the **mammillary peduncle** (*mp*), a tract of fibers that arises by numerous arch-like fibers from the region of the substantia nigra. The fibers appear to come out of the medial border of the **substantia nigra** (*sn*). The lateral border of the medial lemniscus appears to send a large number of terminals into the substantia nigra. Thus the substantia nigra appears to be a **terminus** of some ascending tract in the lateral border of the medial lemniscus, and also the **origin** of the mammillary peduncle which passes up to end in the mammillary nuclei. It is possible that this is a system of gustatory tracts and centers.

Traced upwards (fig. 167) the substantia nigra is replaced by an extensive group of **intrapeduncular nuclei** (*ipn*) of Malone, continued upwards as the **peripeduncular nucleus** (*peri*) of Jacobsohn. The large lateral strio-peduncular tracts (*stp*) end in these nuclei and **not** in the substantia nigra proper. These intrapeduncular nuclei and strio-peduncular tracts cover the dorsal surface of the substantia nigra and have been commonly described as part of it. They are in reality a part of the striatal motor system in which the substantia nigra should probably not be included.

Along the midline (fig. 164) appears the cerebral aqueduct surrounded by central gray matter (*cg*). Ventral to this is the **oculomotor nucleus** (*om*) invaded by a great quantity of collaterals from the large complex **medial longitudinal fasciculus** on each side, which consists of at least five groups of fibers, represented in figure 166. (1) The vestibulo-mesencephalic tracts (*vm*, *cvm*) form a dense *V*-shaped fiber stratum on which the oculomotor nuclei lie. They are here greatly augmented by (2) the tecto-mesencephalic fibers (*tm*) coming from the front part of the tectum, by (3) the fibers of the posterior commissure (*pc*) and interstitial nucleus (*isp*), by (4) the strio-oculomotor tracts (*sto*) connecting the globus pallidus with the oculomotor (*om*), ciliary (*cil*) and interstitial (*is*) nuclei, and by (5) the cerebro-oculomotor tracts coming from the frontal lobe of the cerebral cortex. Collectively these fibers form a dense stratum (fig. 164) that fills the space between the red nucleus and the oculomotor nucleus. The fibers of the **tectospinal tracts** (*ts*) curve through them to decussate (*tsx*) just ventral to the oculomotor nuclei.

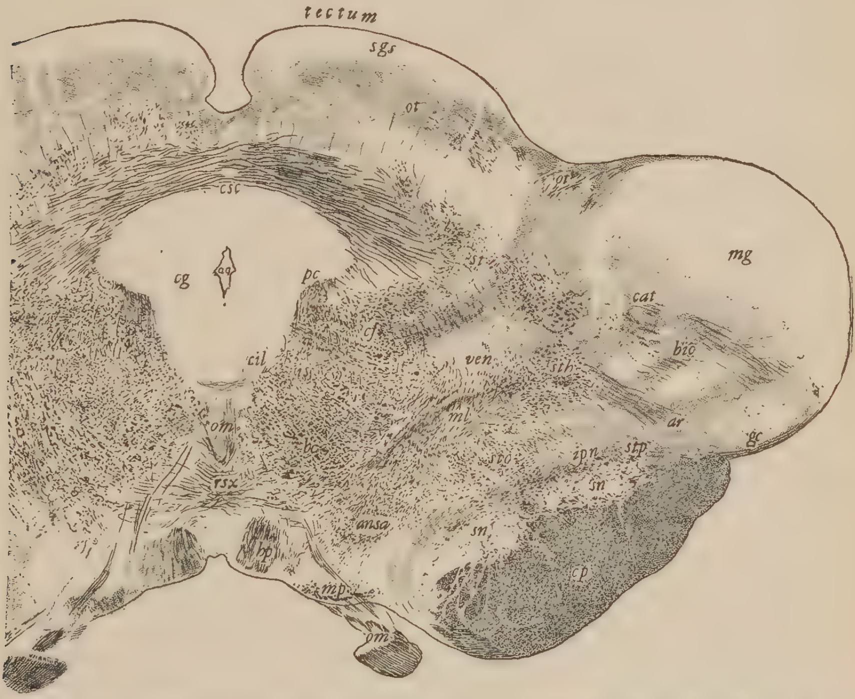

FIG. 165. Section through the upper part of the superior colliculus, cat, × 7½.

These multiple connections of the oculomotor centers through the medial longitudinal fasciculus get a natural explanation when one considers the source of the different responses with which eye movements are combined (fig. 166). (1) The vestibular fibers provide the eye muscle nuclei with tonic impulses and reflex conjugate movements. (2) The tecto-mesencephalic fibers provide impulses for reflex eye movements in response to sight. (3) The fibers of the posterior commissure and interstitio-spinal tracts provide impulses for pupillary and ciliary movements, convergent and divergent movements of the eyes. (4) The strio-oculomotor fibers probably serve to combine eye movements with other instinctive behavioral reactions. (5) The cerebral fibers provide a means for combining eye movements with associational responses (conditioned reflexes).

The **red nucleus** (fig. 165, *rn*) is conspicuous on account of its large cells. Scattered in it are the coarse bundles of the **brachium conjunctivum** which give off collaterals that end around the large cells. The cells of the red nucleus give rise to the **rubrospinal tracts** (*rs*) that decussate in the midline between the red nuclei (*rsx*) and take a position ventral to the red nuclei (*rs*). At a lower level (fig. 163) they turn laterally under the decussation of the brachium conjunctivum and assume a lateral position (fig. 162, *rs*). In this position they descend through the pons, oblongata and cord. It must be remembered that this tract is the chief outlet for impulses from the lateral lobes of the cerebellum (fig. 152). These impulses pass from the Purkinje cells through the dentate nucleus, brachium conjunctivum, red nucleus and rubrospinal tracts to reach the motor nuclei that supply fibers chiefly to the flexor muscles (fig. 152). This circuit is necessary for the smooth and normal regulation of muscle tonus in posture and movement (Magnus). When this circuit is cut there results a stiff, awkward, uncontrolled extensor tonus known as decerebrate rigidity, with a loss of the spontaneous movements in which flexors and extensors no longer coöperate as reciprocal groups.

A section through the upper level of the **tectum** or **superior colliculus** (fig. 165) also cuts through the **medial geniculate body** (*mg*). The **tectum** consists of the same characteristic layers already described: (1) the superficial gray stratum (*sgs*), (2) the stratum of optic tract fibers (*ot*), (3) the spinotectal tract (*st*) whose fibers are now passing forward in the middle gray stratum, and (4) the commissural fibers (*pc*) arching around the central gray (*cg*). The tectospinal fibers that cross the midline form the prominent commissure of the superior colliculus (*csc*).

The **medial geniculate body** (fig. 165, *mg*) is large and uniformly cellular in its outer part. On its ventral surface is a thin layer of

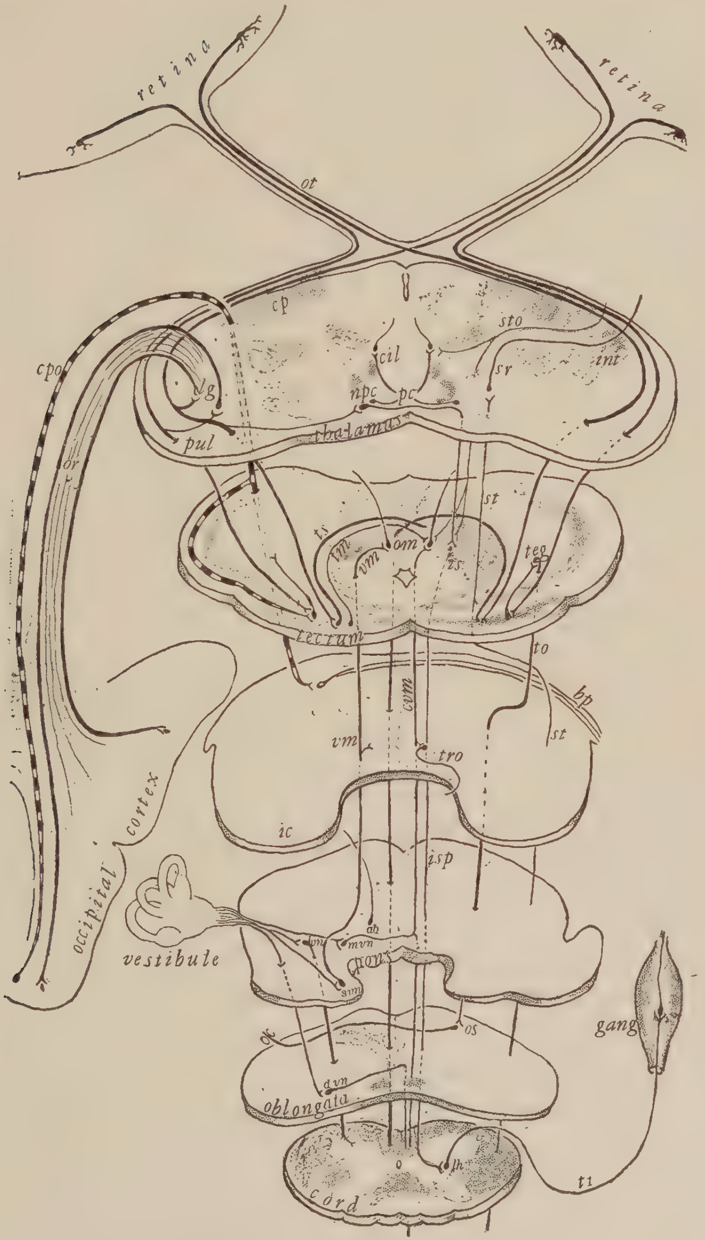

FIG. 166. A plan of the fiber connections of the tectum of the cat.

fibers, the **geniculate commissure** of Gudden (*gc*). On its dorsal surface is the optic tract (*ot*). On its medial surface the **brachium of the inferior colliculus** (*bic*) and the **central acoustic tract** (*cat*) are ending in the geniculate body. Here, too, a nuclear group appears from which the **auditory** thalamo-cortical **radiations** (*ar*) are passing into the ventral side of the geniculate body. This is the first contingent of **sensory radiations of the internal capsule.**

The **spino-thalamic tract** (*sth*) has separated from the medial lemniscus as well as from the central acoustic tract. The **medial lemniscus** (*ml*) is displaced laterally by the red nucleus and its fiber surroundings. Between the lemniscus and cerebral peduncles is the large gray area of fine fibers and cells; these are the **intra-** and **peripeduncular nuclei** (*peri*) and the **strio-peduncular tracts** (*stp*) that end in them. Two remnants of the substantia nigra (*sn*) are seen on the peduncles. Between these a large group of fibers, the **cerebro-oculomotor** and **strio-oculomotor tracts** (*sto*), become detached from the peduncles; at lower levels they shift dorsally to enter the lateral fiber stratum that surrounds the oculomotor nuclei. The **strio-oculomotor tracts** (*sto*) take a more transverse course through this peripeduncular region.

On the midventral surface are seen the **habenulo-peduncular tracts** (*hp*) and lateral to them the mammillary peduncle (*mp*), and the oculomotor nerve root (*om*) on its way out. The **red nucleus** (*rn*) has disappeared, but the fibers of the **brachium conjunctivum** (*bc*) have passed through it to enter the subthalamic region. Here there is a dense fiber stratum consisting, in addition to the brachium conjunctivum (*bc*), of the five fiber groups previously described. The **interstitial nucleus** (*is*) appears in the dorsal part of this fiber stratum. A large tract of fibers, the **posterior commissure** (*pc*), is seen to end in this nucleus (*is*). Between the medial fasciculi are the oculomotor nuclei (*om*). The **ciliary nucleus** (*cil*) is beginning to appear in the central gray just dorsal to the oculomotor and close to the posterior commissure; its fiber connections with surrounding bundles are quite apparent. A delicate *U*-shaped commissure connects the two ciliary nuclei ventral to the oculomotor nuclei. These relations will be seen better in the next section.

Theory of midbrain functions

The tectum is the chief reflex terminus of the optic tracts. In addition, it receives the large bulbo- and spino-tectal tract. The nature of the sensations brought in by this tract is not known. The tectum may be regarded as an important opticosensory center which reflexly regulates the conjugate movements of the eyes; convergence for close vision, divergence for distant vision, ciliary constriction for focusing the eyes on close objects and pupillary movements for regulating the amount of light admitted into the eye. These functions are mediated by the posterior commissure and tecto-mesencephalic tracts that end on the oculomotor, ciliary, interstitial, trochlear and abducens nuclei. Certain lower connections are made through the interstitio-spinal tracts. Through the tecto-spinal tracts the head, trunk and limbs can be moved reflexly in response to light.

The tegmental region contains the large red nuclei which receive the brachia conjunctiva from the dentate nucleus. The red nuclei emit the rubrospinal tracts which regulate the flow of cerebellar impulses into moving muscles.

Important connections of the brachium conjunctivum are effected through the subthalamus with the corpus striatum. In turn the corpus striatum makes connections with the interstitial, ciliary, oculomotor and tegmental nuclei and also with the peripeduncular, intrapeduncular, masticator and facial nuclei.

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CHAPTER 29

STRUCTURE OF THE THALAMUS (DIENCEPHALON)

THE **thalamus** proper consists of a group of large nuclei which receive the large sensory tracts and radiate fibers to different regions of the cerebral cortex. On the brain stem (figs. 78, 79) determine the structures that would be cut at this level. On the dorsal surface is the pineal body (*pin*); ventral to it joining the two thalamic masses is the **posterior commissure** (*pc*). Lateral to this and posterior to the habenular bodies note the slightly raised area. This is the nucleus of the **posterior commissure.** The anterior end of the superficial gray stratum (*sc*) overlies this area. More laterally is the large pulvinar (*pul*) overspread by fibers of the optic tract (*ot*), the optic stratum, as it enters the colliculus. On the lateral surface the lateral geniculate body (*lg*) forms a prominent bulging, and the **optic tract** is seen spreading over it as the optic stratum. Posterior to the optic tract note the **medial geniculate body** (*mg*). On the ventral surface (figs. 73, 74) note the cerebral peduncles (*cp*). Between them is the interpeduncular fossa occupied by the mammillary bodies (*mb*) and tuber cinereum (*tc*). Examine a brain cut in a median sagittal section (fig. 77) and note the position of the posterior commissure. Note how the cerebral aqueduct expands here to join the third ventricle.

In sections through the posterior commissure (fig. 167, *pc*) the **pineal body** (*pin*) is seen on the dorsal side. It is unstained and contains no nervous tissue. On each side is a remnant of the **superficial gray stratum** (*sgs*) of the superior colliculus. Ventral to this note the deep layer of fibers, the **optic stratum** (*ot*). More laterally you will see the densely stained optic tract (*ot*) as it enters this stratum by passing over the **medial geniculate body** (*mg*). Ventral to the optic stratum find the nucleus of the optic tract (*not*). Here it occupies a more medial position than the same layer (*mgs*) did in the brain, and closely approaches and merges with the nucleus of the posterior commissure (*npc*).

In the midline dorsal to the aqueduct note the **posterior commissure** (*pc*) and on each side of it a diffuse nuclear mass, the **nucleus of the posterior commissure** (*npc*). Its dorsal part receives many optic fibers. Its center is occupied by fibers that are an upward continuation of the **spino-tectal tract** (*st*). From its lateral side a tract of fibers is seen to arise and pass laterally towards the **internal capsule** (*int*). The fibers of the posterior commissure (*pc*) arise from this nucleus (*npc*), at least in large part, and cross through the commissure to end in the ciliary nucleus (*cil*) as well as in the nucleus of the medial longitudinal fasciculus, also called the **interstitial nucleus** (fig. 165, *is*).

The interstitial nucleus (*is*) gives rise to the **interstitio-spinal tract** that descends without crossing with the tectospinal tract (fig. 166, *isp*). It should be noted that the optic tract ends in the nucleus of the posterior commissure (*npc*) and that the **spinotectal tract** (*st*) also comes up from the oblongata and cord to end in it. The latter (*st*) probably conducts cutaneous sensibility to and through the tectum (superior colliculus) and then ends in the nucleus of the posterior commissure (*npc*). Fibers from this nucleus form the commissure (*pc*) and turn ventrally to end on the interstitial nucleus (*is*). The ciliary and the interstitial nuclei also receive from the globus pallidus the strio-oculomotor fibers (*sto*). It (*is*) gives rise to the interstitio-spinal tract. It seems probable that these connections mediate ciliary and eye movements in response to contacts or sight. Thus a contact with the right face would pass up by the left spinotectal tract (*st*) to the tectum which would produce a movement of the head and eyes to the right side through the right tecto- and interstitio-spinal tracts. Optic impulses would produce a like result.

The **tecto-mesencephalic fibers** (*tm*) arise from the tectum just as the tectospinal fibers with which they curve into the region of the oculomotor nucleus (*om*). Since most of this nucleus (*om*) and the **ciliary nucleus** (*cil*) lie higher up in the midbrain, the tecto-mesencephalic fibers have to turn up in the medial longitudinal fasciculus for a short distance and then hook into these motor nuclei (fig. 167). In the cat the ciliary nucleus is very large and the tecto-mesencephalic fibers that enter it from the medial longitudinal fasciculus are clearly seen hooking around the **habenulo-peduncular tract** (*hp*). A delicate commissure connects the ciliary nuclei.

Lateral to the nucleus of the posterior commissure is the posterior or **central nucleus** (*cnt*) of the thalamus. A large tract of fibers from the central tegmental fasciculus (*cf*) ends in this nucleus. **Thalamo-cortical fibers** arise from it and pass ventrally and laterally through the arcuate nucleus (*arc*) to enter the internal capsule (*int*). Other heavier fibers pass ventromedially and downward into the red nucleus; this is one of the first groups of fibers to become myelinated in the kitten. The central nucleus is the only thalamic nucleus that has such a connection. In this region the central nucleus (*cnt*) and the nucleus of the posterior commissure (*npc*) are the two thalamic centers that appear to have reflex motor connections in addition to the thalamo-cortical radiations.

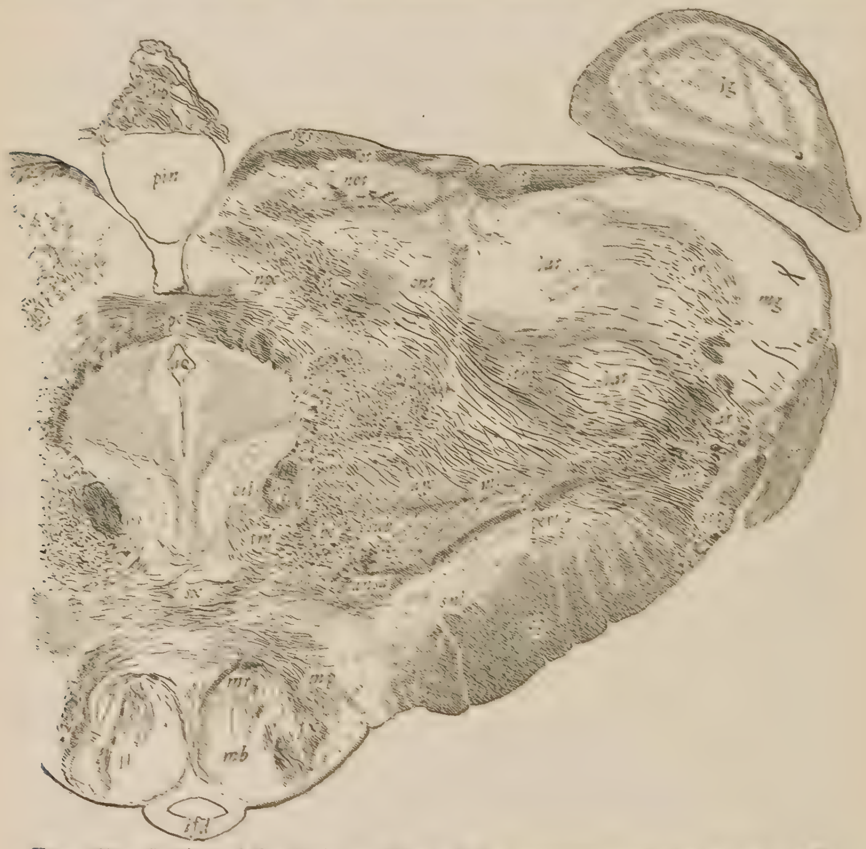

FIG. 167. Section of the thalamus through the posterior commissure, cat, × 7½.

The **medial geniculate body** (*mg*), an auditory relay center, forms a large cellular crescent on the lateral surface. It encloses the **lateral nucleus of the thalamus** (*lat*) which is divisible into a dorsal and a ventral part. There is no true separation of these from each other and only an indefinite one from the medial geniculate body. They are all differentiated from a common lateral thalamic mass of cells. In the medial side of these nuclei (*lat*) is seen the diffuse ending of the **spino-thalamic tract** (*sth*). On their lateral side the auditory (*ar*) and sensory radiations (*sr*) are seen passing up to the internal capsule. Ventral to them near the **cerebral peduncles** (*cp*) is seen the **internal capsule** (*int*) into which converges all the thalamo-cortical fibers coming from the thalamic nuclei at this level. The lateral thalamic nuclei probably relay cutaneous sensibility to the parietal cortex.

The ventral-lateral or **arcuate nucleus of the thalamus** (*arc*) extends medially as a hook from the lateral nucleus and lies ventral to the central nucleus (*cnt*) which sends many fibers through it to reach the internal capsule (*int*). The medial lemniscus (*ml*) ends in this arcuate nucleus, passing along its ventral border, and discharges into it impulses of proprioceptive sensibility. The nucleus gives origin to **thalamo-cortical fibers** that pass ventrally and laterally into the internal capsule (*int*) to end in the coronal (postcentral) gyrus of the cerebral cortex. Similar fibers from the central nucleus and nucleus of the posterior commissure cut through the arcuate nucleus on their way to the internal capsule and thence to the cortex.

In the **subthalamic region** ventral to the medial lemniscus (*ml*) is the subthalamic terminus of the **brachium conjunctivum** (*bc*) ending under the arcuate nucleus in a group of scattered cells, the **reticular subthalamic nucleus** (*sub*) or zona incerta of Forel's dorsal field. A small commissure (*sx*) unites the two subthalamic regions. From the reticular subthalamic nucleus fibers which collectively form the **thalamic fasciculus** (*tf*) pass laterally just under the arcuate nucleus (*arc*) and the medial lemniscus (*ml*) and join the internal capsule (*int*) to end in the putamen. These fibers (*tf*) are seen crossing through the thalamo-cortical radiations. The **strio-oculomotor** fibers and **strio-peduncular** (*stp*) are seen over the lateral border of the peduncles. The curves they make over the lateral border of the peduncles are obscured here by the internal capsule. They (*stp*) are ending in the peripeduncular (*peri*) nuclei. The transverse peduncular tract (fig. 160, *tp*) arises in this region and passes around the medial border of the peduncles and over their external surface to end in the tectum.

The **hypothalamus** (fig. 167) is a name applied to the mammillary bodies, tuber cinereum and other related structures between the cerebral peduncles and subthalamic regions. The **mammillary bodies** (*mb*) consist of a large medial and a smaller lateral mammillary nucleus. The **mammillo-thalamic tract** (*mt*) is seen arising from the medial one; and the column of the **fornix** (*fx*) is seen ending in the lateral one which is sending fibers into the medial one.

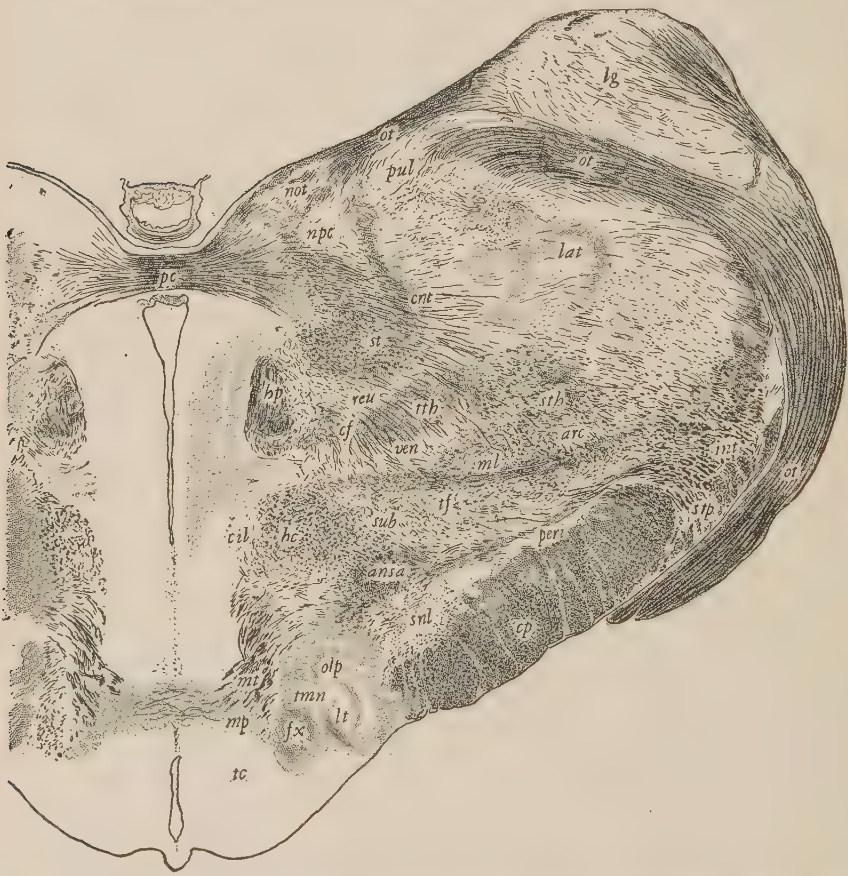

FIG. 168. Section of the thalamus just above the posterior commissure, cat, × 7½.

On the lateral surface is the **mammillary peduncle** (*mp*) ending in the mammillary nuclei and in the nucleus that surrounds the mammillary body on the lateral, dorsal and anterior side. These tracts are seen ending just dorsal to the mammillary bodies, ventral to the commissure (*sx*).

A section through the front end of the posterior commissure (fig. 168, *pc*) shows that it takes origin from the nucleus of the posterior commissure (*npc*) on each side. Ending in the nucleus is seen the

spino-tectal tract *(st)* and leaving the nucleus in a ventral and lateral direction are its thalamo-cortical fibers that cut through the ventral nucleus *(ven)* on their way to join the internal capsule *(int)*. It is seen that the **nucleus of the optic tract** *(not)* has joined that of the posterior commissure, and that the **optic tract** *(ot)* is sending many fibers into both nuclei. The central nucleus *(cnt)* has almost disappeared. In its place appears the **nucleus reuniens** *(reu)* in which is ending the **central tegmental fasciculus** *(cf)* and from which arise many thalamo-cortical radiations going to the internal capsule *(int)*. Medial to both is the **habenulo-peduncular tract** *(hp)*. Ventral to this is a clear nucleus which forms the medial tip of the ventral nucleus. The tecto-mesencephalic fibers *(tm)* passing to the ciliary nucleus *(cil)* have nearly disappeared.

The **lateral nucleus** *(lat)* is now of great size. The spino-thalamic tracts *(sth)* are still seen in its medial concave side. The nucleus is giving off a great quantity of thalamo-cortical fibers that pass ventrally into the internal capsule *(int)*. The **arcuate nucleus** *(arc)* forms the small medial hook under the ventral nucleus which is now replacing it. The medial lemniscus *(ml)* is ending in the arcuate nucleus and numerous thalamo-cortical radiations pass from it into the internal capsule *(int)*.

The **ventral nucleus** *(ven)* is now appearing between the arcuate nucleus *(arc)* and the reuniens *(reu)*. Its medial ventral part is a clear crescent, but its dorsal surface is filled with a large tract *(tth)* that has come up with the medial lemniscus and has separated from it to enter the ventral nucleus.

The optic tract *(ot)* surrounds the cerebral peduncles *(cp)* and internal capsule *(int)* and ends in the **lateral geniculate body** *(lg)*. Note the layers of cells in this nucleus. A part of the tract is continued over the surface to end in the **pulvinar** *(pul)* and **nucleus of the posterior commissure** *(npc)*. The pulvinar is small in the cat. It is differentiated from the dorsal part of the lateral nucleus. Great quantities of **optic thalamo-cortical radiations** are seen in the pulvinar and lateral geniculate body. They will pass into the internal capsule at higher levels. The large band of optic fibers *(ot)* between the lateral geniculate body *(lg)* and lateral nucleus *(lat)* are passing down into the optic stratum of the superior colliculus.

The **subthalamus** is separated from the ventral nucleus *(ven)*, from the arcuate nucleus *(arc)* and from the medial lemniscus *(ml)* by a wing-like band of fibers, the **thalamic fasciculus** *(tf)*, which contains within it the reticular subthalamic nucleus (*sub*). The fibers of the thalamic fasciculus (*tf*) come from the **reticular subthalamic nucleus** (*sub*) which receives the subthalamic terminus of the brachium conjunctivum (*bc*), still seen as a large bundle on the medial side. Ventral to this is the ansa lenticularis (*ansa*). Lying on the medial side of the peduncles is the **subthalamic nucleus** of Luys (*snl*) which receives many strio-subthalamic fibers. More laterally is the peripeduncular nucleus (*peri*).

In the **hypothalamus** between the cerebral peduncles is the **tuber cinereum** (*tc*). In its dorsal part is the **mammillo-thalamic tract** (*mt*) of Vicq d'Azyr. In its lateral part is the column of the fornix (*fx*) on its way down to end in the mammillary body. Lateral to both of these tracts is the diffuse **tubero-mammillary nucleus** (*tmn*) infiltrated by fine fibers, probably terminals of the olfacto-peduncular tract (*olp*). The connections of the tubero-mammillary nucleus are uncertain, but it appears to stand in intimate relation with the main fiber bundles of this region, namely, the mammillary peduncle (*mp*), the fornix (*fx*), mammillo-thalamic tract (*mt*), the ansa lenticularis (*ansa*) and the olfacto-peduncular tract (*olp*). The fibers (*olp*) nearer the cerebral peduncles appear to be chiefly concerned. They can be traced as far forward as the nucleus of the olfactory tubercle, or olfactory striatum (fig. 172, *ost*) from which they appear to arise. For this reason they may be called the **olfacto-peduncular tract** (*olp*) comparable to the strio-thalamic or medial basal forebrain bundle of lower vertebrates. A small, compact, lateral nucleus of the tuber (fig. 168, *lt*) is situated in this tract. This nucleus attains a great size in the Primates (see page 473).

In sections (fig. 169) through the habenular region, the thalamic nuclei have a typical arrangement. The **habenular body** (*hb*) consists of a medial and a lateral habenular nucleus. In their dorsal margin is the **olfacto-habenular tract** or medullary stria (*oh*) which ends in these nuclei. This is an olfactory connection of great antiquity, being prominent in Fishes. It is found in all true vertebrates.

A schema of the olfactory connections is shown in figure 175. It will be seen that the olfactory bulb projects upon the medial olfactory area and olfactory tubercle. From these regions three systems of fibers arise. From the medial area (*sep*) the septo-hippocampal fibers (*ols, sh*) pass back to the hippocampus. From the region of the olfactory tubercle (*ost*) the olfacto-peduncular fibers (*olp*) pass down to the tubero-mammillary nucleus (*tmn*). From the same region the olfacto-habenular fibers (*oh*) pass dorsally to end in the habenular body (*hb*). The **habenulo-peduncular tract** (*hp*) arises from the lateral habenular nucleus, and passes ventrally near the midline (figs. 167, 168) and crosses through the medial anterior side

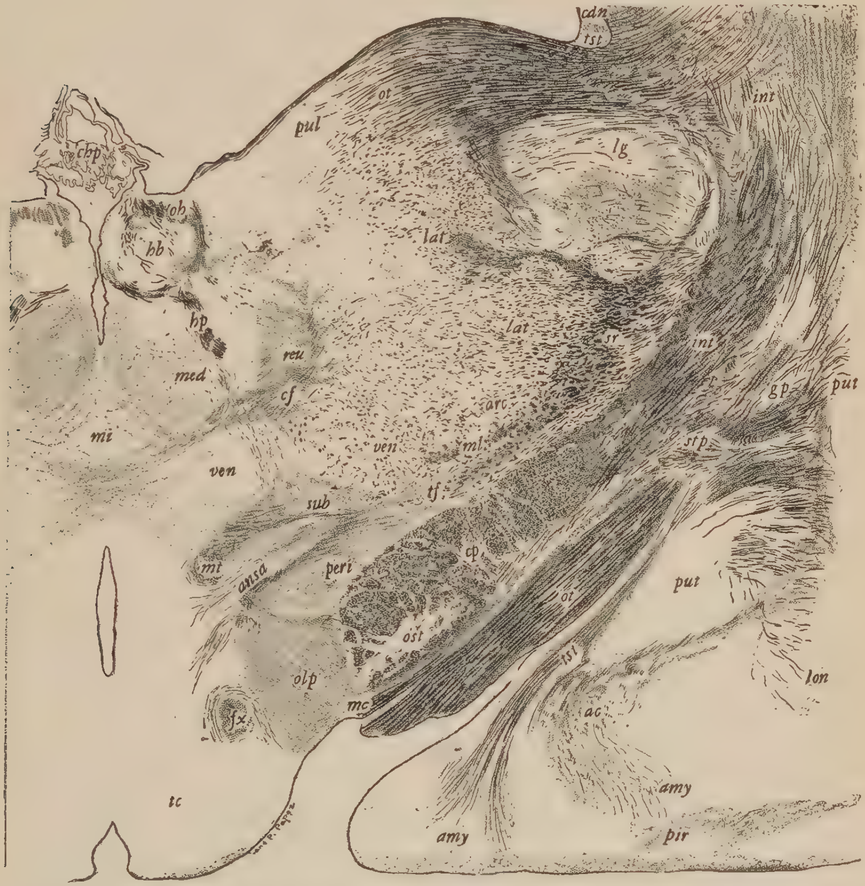

FIG. 169. Section of the thalamus through the habenular region, cat, × 7½.

of the red nucleus. Along the ventral surface, in the interpeduncular region (fig. 165) it passes down to end in the interpeduncular nucleus (fig. 164). From this nucleus fibers pass dorsally along the raphe to reach the dorsal tegmental nucleus of Gudden (*stn*) and probably also the nucleus incertus. These seem to connect with the reticular nuclei. The function of this system is obscure, though generally regarded as having some motor significance.

The medial nucleus (fig. 169, *med*) of the thalamus lies ventral to the habenular nuclei and surrounds the habenulo-peduncular tract. Its position is in front of the nucleus of the posterior commissure which it has replaced. The **nucleus reuniens** (*reu*) surrounds it (*med*) on its lateral and ventral side. In the reuniens nucleus ends the central tegmental fasciculus (*cf*). It appears also to end in the medial nucleus. From it arise a large number of the thalamo-cortical fibers. Note that the nucleus reuniens joins with its fellow of the other side through the soft commissure or massa intermedia (*mi*), as a triangular nucleus.

The tip of the ventral nucleus (*ven*), quite clear of fibers in its medial part, extends into the ventral part of the massa intermedia (*mi*). A distinct line of fibers, formed by the thalamic fasciculus (*tf*) and medial lemniscus (*ml*) separates the ventral nucleus (*ven*) from the subthalamic region. The **lateral nucleus** (*lat*) is large. Its ventral border has fused with the arcuate nucleus and is crossed by great numbers of thalamo-cortical radiations (*sr*) on their way to the internal capsule (*int*). The **pulvinar** (*pul*) is the dorsal part of the lateral nucleus. The **optic tract** (*ot*) passes ventral to the peduncles. Its terminal portion is seen ending in the **lateral geniculate body** (*lg*) and pulvinar (*pul*). The commissure of Meynert (*mc*) is seen passing between the peduncles and the optic tract. More laterally is the globus pallidus (*gp*) giving rise to the strio-peduncular fibers (*stp*) and ansa lenticularis.

In the **subthalamic region** the **mammillo-thalamic tract** (*mt*) is sending a spray of fibers into a special part of the **reticular subthalamic nucleus** (*sub*), which is still sending fibers, the **thalamic fasciculus** (*tf*), laterally to enter the corpus striatum. The thalamic terminus of the brachium conjunctivum has disappeared (*tf*). More ventrally is the ansa lenticularis (*ansa*). This is in relation to an extensive diffuse peripeduncular nucleus (*peri*) which covers the dorsal surface of the peduncles. In it quantities of fine striosubthalamic fibers are seen. Note the columns of the fornix (*fx*). The olfacto-peduncular tracts (*olp*) are seen medial to the cerebral peduncles infiltrating the tubero-mammillary nucleus (*tmn*).

In sections through the middle of the thalamus (fig. 170) the **lateral geniculate body** (*lg*) disappears. It is surrounded by a great quantity of **optic thalamo-cortical fibers** (*or*) which also come from the pulvinar. They form here the dorsal part of the internal capsule (*int*). The ventral part is formed by the auditory, kinesthetic (*sr*) and by other radiations coming from the medial geniculate body, nucleus of the posterior commissure, lateral, arcuate and reuniens nuclei of the thalamus. The lateral nucleus (*lat*) is still large. The pulvinar is replaced by the clear dorsal part (*dor*) of the lateral nucleus.

The large **ventral** (*ven*) and **arcuate** (*arc*) nuclei rest almost on the peduncles. They are filled with great numbers of thalamo-cortical bundles (*or*, *sr*) that pass forward and shift laterally into the internal capsule (*int*). The border zone along the internal capsule is often spoken of as the reticular nucleus. The **nucleus reuniens** (*reu*) is more extensive and diffuse, and infiltrates the medial border of the ventral and lateral nuclei. The **olfacto-habenular tracts** (*oh*) pass in the dorsal medial border. Ventral to them is the **clear medial nucleus** (*med*) surrounded by the reuniens which gives rise to a scattered bundle of fibers that passes forward

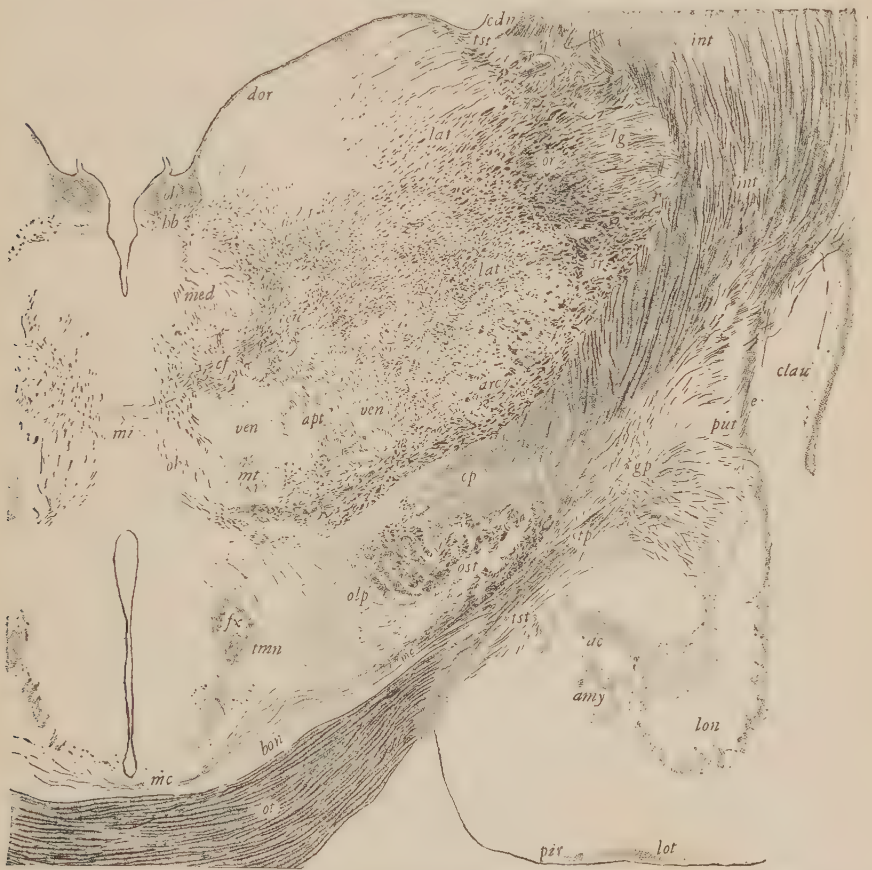

FIG. 170. Section through the middle of the thalamus and optic chiasma, cat, × 7½.

and ventrally through the ventral nucleus to form the anterior peduncle of the thalamus (*apt*). The ventral and reuniens nuclei are regarded as relay centers for trigeminal (facial) sensibility. Fibers in the medial nucleus are seen to pass dorsally medial to the ventral nucleus as the olfacto-habenular tract (*oh*). They turn laterally through the cerebral peduncle to reach the olfactory tubercle. It is this band of fibers through the medial nucleus that is sometimes designated as the ansa peduncularis.

The **cerebral peduncles** (*cp*) are medial to the internal capsule. In their ventral border the **peduncular nucleus** (*ost*) and **olfacto-peduncular** (*olp*) are seen. External to the capsule is seen the globus pallidus (*gp*) which gives rise to (1) the **ansa lenticularis fibers** (fig. 168, *ansa*) that pass around the ventral border of the peduncles, (2) the **strio-subthalamic fibers** that pass through the peduncles to the subthalamic nucleus of Luys (*snl*) and (3) the **strio-peduncular tracts** (*stp*) that pass down into the peripeduncular (*peri*) and intra-peduncular nuclei which surround the substantia nigra at lower levels. In this region (fig. 170) the typical subthalamic structures have nearly disappeared.

The chiasma or crossing of the **optic tracts** (*ot*) surrounds the ventral surface of this region. In its dorsal surface are seen fibers of Meynert's commissure (*mc*) which connects the ~~globus~~ pallidus of one side with its fellow of the other side. The hypothalamic commissure of arching fibers connects the olfactory striatum (*ost*) with its fellow. The **tubero-mammillary nucleus** (*tmn*) is seen lateral to the column of the fornix (*fx*). The **mammillo-thalamic tract** (*mt*) is seen in the tip of the ventral nucleus. The **basal optic nucleus** (*bon*) is a group of large cells seen on the surface under the lateral border of the optic chiasma. Fine myelinated fibers stream dorsally through the **olfacto-peduncular fibers** (*olp*). In the wall of the ventricle is seen the **paraventricular nucleus** of Malone. It corresponds to the preoptic nucleus of lower vertebrates. In the Fishes this nucleus sends fibers to the vascular sac of the hypothalamus (see page 473).

In sections through the anterior part of the thalamus (fig. 171) the **lateral nucleus** (*lat*) is still prominent as it lies against the large internal capsule (*int*). It is filled with a great quantity of thalamo-cortical fibers (*sr*), most of which have accumulated on the inner surface of the internal capsule (*int*). The ventral nucleus is replaced by a large tract of fibers, the anterior peduncle of the thalamus (*apt*) which passes to the subcentral region or the diagonal gyrus. On the dorsal surface now appears the **dorsal nucleus** (*dor*) which forms the anterior tubercle of the thalamus. This nucleus sends its fibers laterally and forward into the internal capsule. The large **anterior nucleus** (*ant*) is ventral to the dorsal and replaces the anterior end of the medial nucleus. It is large in the lower animals. Around this nucleus ends the mammillo-thalamic tract (*mt*). This nucleus gives rise to the fibers which are described as passing over the surface of the dorsal nucleus to reach the head of the caudate (*cdn*). Ventral to the medial nucleus is the column of the fornix (*fx*), and the olfacto-habenular tracts (*oh*) that come from the region of the olfactory striatum (*ost*).

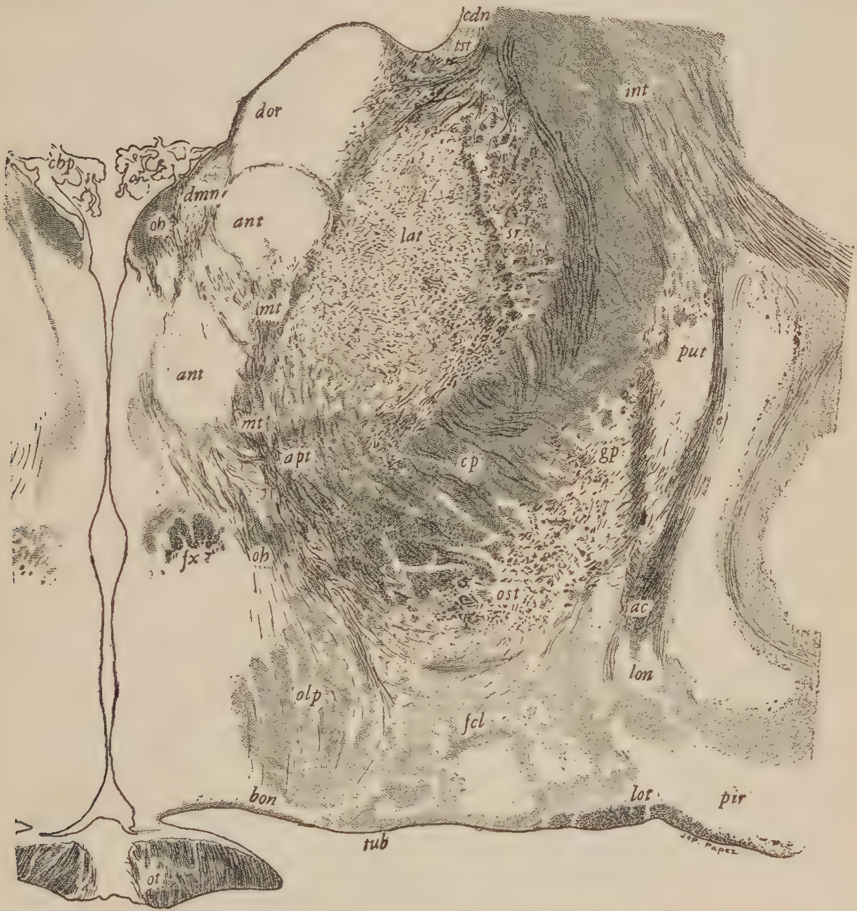

Fig. 171. Section through the anterior part of the thalamus, cat, × 7½.

Along the dorsal midline is the **olfacto-habenular tract** (*oh*). Between it and the dorsal and anterior nuclei is a small triangular dorsal medial nucleus (*dmn*) that appears to be related to both nuclei. It lies against the anterior nucleus and sends fibers over the dorsal nucleus, and receives fibers from the olfacto-habenular tract (*oh*). It is relatively large in the lower mammals.

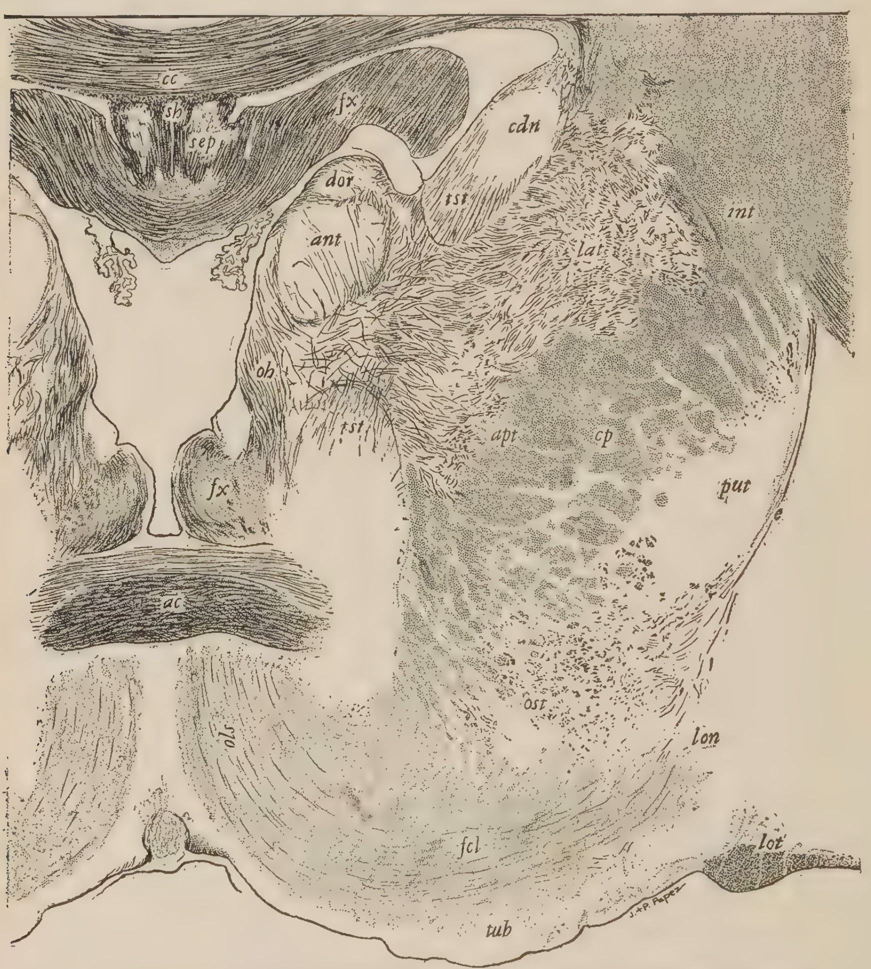

FIG. 172. Section through the anterior commissure just above thalamus, cat, × 7½.

The ventral surface is formed by the olfactory tubercle (*tub*) and the anterior perforated area, also an olfactory cortex (*fcl*) with several islands of cells. The **olfacto-peduncular tracts** (*olp*) are seen in their medial side. The fibers of the olfacto-habenular tract (*oh*) are seen curving through the cerebral peduncles.

In a section through the anterior commissure (fig. 172, *ac*) the thalami nuclei disappear and are replaced by the dense anterior limb of the **internal capsule** (*int*) and the anterior peduncle of the thalamus (*apt*). The terminal stria (*tst*) and caudate nucleus (*cdn*) are seen on the lateral side. The stria (*tst*) is seen to end in the clear bed nucleus around the anterior commissure (*ac*). The olfacto-habenular tracts (*oh*) are joined by fibers of the fornix (*fx*) and also those from the region of the olfactory striatum (*ost*) of the previous section (fig. 171). The columna of the fornix (*fx*) cross over the **anterior commissure** (*ac*) to curve dorsally and unite with the bodies of the fornix. In the peduncles (*cp*) the **striate body** (*ost*) has become a conspicuous structure. The clear segment on the lateral side is the **putamen** (*put*). The gray masses within the peduncle constitute the beginning of the globus pallidus (*gp*). Its continuity with the olfactory striatum or peduncular nucleus (*ost*) is seen in this region.

Summary of connections of thalamic nuclei

1. Nucleus of posterior commissure: Afferent, spinotectal tract. Efferent, posterior commissure to interstitial nucleus and thalamo-cortical fibers to cortex. Optic reflexes and cutaneous sensibility.
2. Medial geniculate body: Afferent, brachium of inferior colliculus and central acoustic tract. Efferent, auditory thalamo-cortical radiations to sylvian gyrus. Hearing.
3. Lateral geniculate body: Afferent, optic tracts. Efferent, optic radiations to visual area. Vision.
4. Pulvinar: Afferent, optic tracts as lateral zone of Wernicke. Efferent, optic radiations to visual area in occipital cortex. Vision. Probably color vision.
5. Central nucleus of Luys: Afferent, central tegmental tract. Efferent, thalamo-cortical radiations and fibers to red nucleus. Cutaneous sensibility, with motor reactions.
6. Nucleus reuniens: Afferent, central tegmental tract. Efferent, thalamo-cortical radiations. Cutaneous sensibility probably from face.
7. Arcuate nucleus: Afferent, gracilo- and cuneo-thalamic tracts. Efferent, thalamo-cortical radiations to postcentral or coronal gyrus. Deep sensibility.
8. Lateral nucleus: Afferent, spinothalamic tract. Efferent, thalamo-cortical to parietal region. Cutaneous sensibility from body and limbs.

9. Ventral nucleus: Afferent, pontal trigemino-thalamic tract. Efferent, anterior peduncle of thalamus, probably to subcentral region around diagonal sulcus. Facial sensibility.

10. Medial nucleus: Afferent, central tegmental tract. Efferent, anterior peduncle of thalamus to cortex. Possibly pain or affective sensibility?

11. Anterior nucleus: Afferent, mammillo-thalamic tract. Efferent, tract to caudate nucleus. Feeding reactions?

12. Dorsal medial nucleus: Afferent, from preoptic region? Efferent, ansa peduncularis to olfactory tubercle and piriform cortex and probably connection with septum?

13. Habenular nuclei: Afferent, olfacto-habenular tract. Efferent, habenulo-peduncular tract to interpeduncular nucleus, then to dorsal tegmental nucleus. Smell reactions?

14. Mammillary nuclei: Afferent, fornix from hippocampus and mammillary peduncle from region of substantia nigra. Efferent, mammillo-thalamic tract to anterior part of reticular subthalamic nucleus and to anterior nucleus of thalamus, thence, fibers to caudate nucleus. Subcortical feeding reactions?

15. Tubero-mammillary nucleus: Afferent, olfacto-peduncular tract from region of olfactory tubercle, and ansa lenticularis. Efferent connection unknown, possibly Gudden's tract down to the reticular nuclei.

16. Reticular subthalamic nucleus: Afferent, thalamic terminal fibers of brachium conjunctivum, also collaterals of mammillo-thalamic tract to its anterior dorsal part. Efferent, thalamic fasciculus to corpus striatum. Stereotyped motor reactions dealing with compound associated movements.

17. Subthalamic nucleus of Luys, peripeduncular, intrapeduncular and perinigric nuclei: Afferent, striopeduncular fibers from the globus pallidus. Efferent, fibers into the cerebral peduncles and reticular formation, probably to pons and cerebellum. Instinctive reactions, compound purposive, associated movements, feeding, nursing, laughing, crying, playing, etc.?

18. Paraventricular nucleus: Afferent fibers from olfactory region. Efferent to infundibulum and hypophysis cerebri?

Theory of thalamic function

The thalamus is the internode through which the cerebral cortex, the olfactory brain and the hippocampus and the corpus striatum get into connection with the subcortical centers and conduction systems.

1. The sensory nuclei of the thalamus proper receive the endings of the great sensory pathways, the spinothalamic, spinotectal and optic tracts, the medial and lateral lemnisci and the central tegmental fasciculus; and they emit the great thalamo-cortical radiations that distribute to various sensory areas of the cerebral cortex which they irradiate with their appropriate impulses. Since all the sensory thalamic nuclei have a demonstrable cortical connection, the

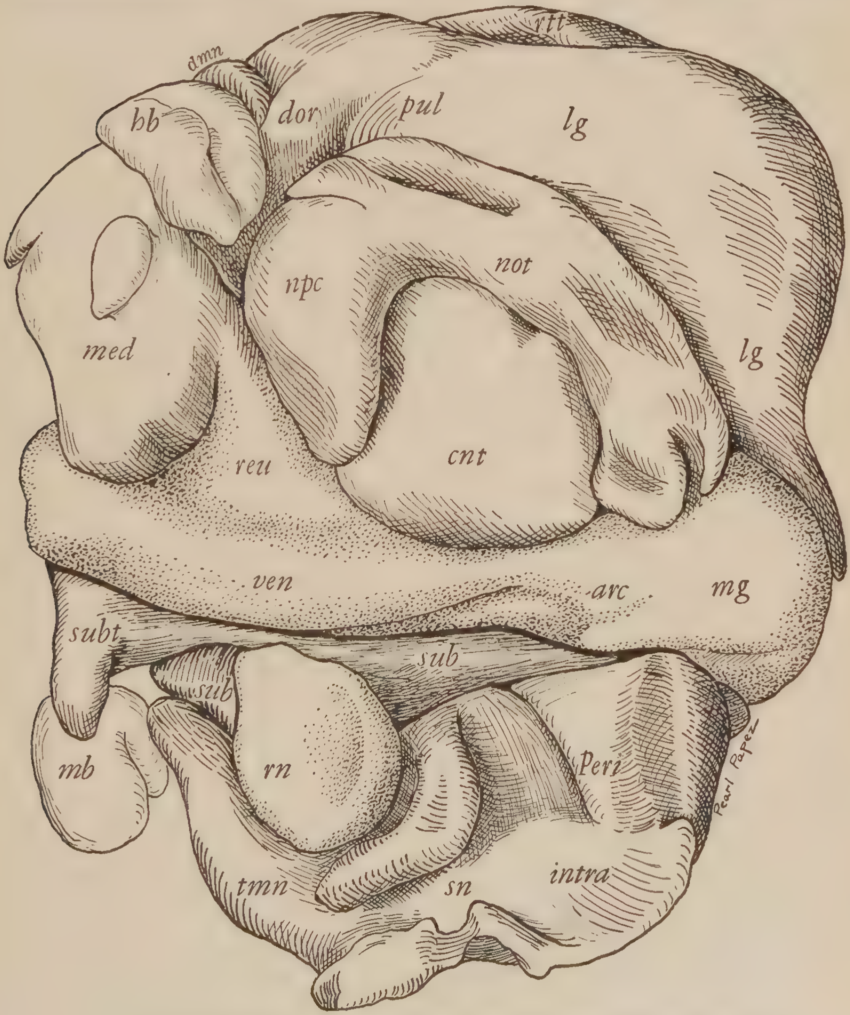

Fig. 173. Model of thalamic nuclei of the sheep, posterior dorsal view, × 7½.

view that the thalamus is the sole seat of pain and affective responses can not be sustained.

2. The subthalamus in like manner effects connections with the corpus striatum. The reticular subthalamic nucleus and adjacent masses receive the terminus of the brachium conjunctivum, also collaterals from the mammillo-thalamic fasciculus and possibly also fibers from the tubero-mammillary nucleus and fibers of the olfacto-peduncular tract. It sends the thalamic fasciculus laterally to the corpus striatum. On the other hand the strio-peduncular, strio-subthalamic and strio-oculomotor fibers pass down to the subthalamic, peripeduncular, intrapeduncular and perinigric nuclei, and through them effect motor connections with the lower reflex motor mechanisms. Certain of the instinctive responses, or complex associated purposive movements are released by this system.

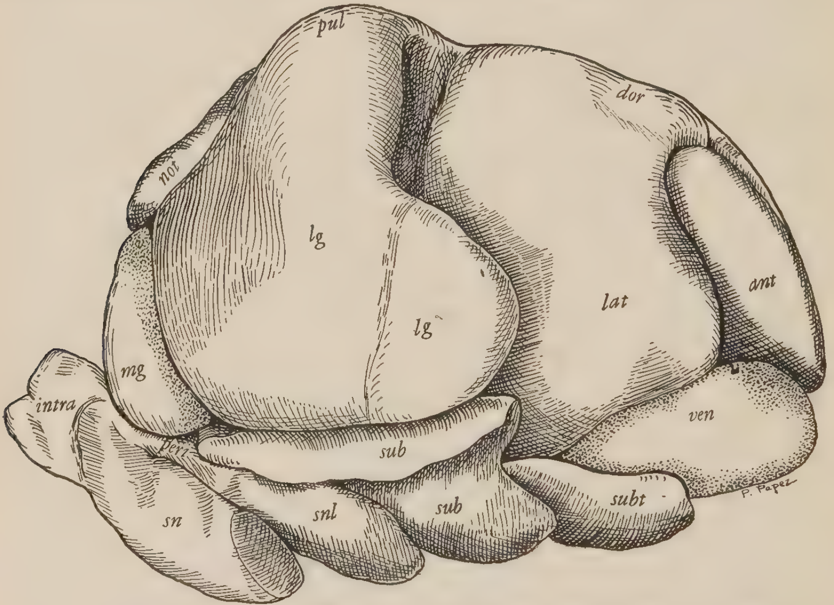

FIG. 174. Model of the thalamic nuclei of the sheep, ventral anterior view, × 5.

3. The hypothalamus probably deals with the feeding and metabolic functions. It receives through the fornix olfactory excitations which it transmits through the mammillo-thalamic tract and other connections to the corpus striatum and probably also to the piriform and adjacent cortex. From the peduncular region it receives the mammillary peduncle which probably brings in gustatory excitations.

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CHAPTER 30

STRUCTURE OF THE STRIATE BODY

THE striate body consists of the **caudate** (*cdn*) and **lentiform** (*put*) **nuclei** separated by the internal capsule (*int*). From the capsule numerous small fiber bundles radiate laterally into the lentiform nucleus and upward into the caudate giving them a striated appearance. In lower mammals the internal capsule is reduced in size and takes a more scattered course through the nuclei.

Two divisions of the striate body may be recognized, the upper olfactory striatum (*ost*) related to the olfactory tubercle (*tub*) and the lower striatum connected with the subthalamic region.

1. The lentiform (*put*) and caudate (*cdn*) nuclei are united around the anterior ventral border of the internal capsule (fig. 177) and come into direct relation with the olfactory tubercle (*tub*) and anterior perforated substance. Here their ventral parts effect olfactory connections and become the **motor olfactory striatum** (*ost*) which descends as the peduncular nucleus and gives rise to the olfacto-peduncular tracts (*olp*) and hypothalamic commissure.

2. At lower levels (fig. 169) the putamen receives the thalamic fasciculus (*tf*) from the reticular subthalamic nucleus (*sub*). This nucleus consists of two parts: the upper part receives the collaterals of the thalamo-mammillary tract (taste and hippocampal excitations); the lower part receives the thalamic terminals of the brachium conjunctivum (motor excitations from the cerebellum). The **globus pallidus** is the motor nucleus of the lower striatum and gives rise to the strio-oculomotor, strio-peduncular, ansa lenticularis and strio-bulbar tracts which end in the oculomotor, ciliary, subthalamic, peripeduncular, intrapeduncular, tegmental, tubero-mammillary, masticator and facial nuclei, and to Meynert's commissure.

The olfactory striatum

Examine the region of the olfactory striatum first. The head of the **caudate nucleus** (*cdn*) is a prominent clear mass of cells on the inner surface of the internal capsule (fig. 179) where it occupies the anterior horn of the ventricle. The medial wall here is formed by the preterminal area or **subcallosal gyrus** (32). In the ventral part is seen the ventricular extension into the olfactory peduncle; and adjoining it the **anterior commissure** (*ac*). On the ventral surface is the **lateral olfactory tract** (*lot*) and rhinal fissure (*rf*). Dorsally the **corpus callosum** (*cc*) unites the two hemispheres.

In a section at a lower level (fig. 178) the **putamen** (*put*) of the lentiform nucleus appears on the later side of the internal capsule (*int*) and joins with the caudate and hooks up into the preterminal region (32). The surface of this region is joining the olfactory tubercle. In the gyrus subcallosum (32) the olfacto-septal (*ols*) fibers are seen passing dorsally to join the septal nuclei (*sep*) and septo-hippocampal tract (*sh*) under the corpus callosum. On the ventral surface is seen the lateral **olfactory tract** (*lot*), **piriform area** (*pir*) and **rhinal fissure** (*rf*). The ventral part of the striatum (*ost*) is clearly related to the olfactory tubercle and contains within it the **anterior commissure** (*ac*) coming from the interior of the olfactory bulb. Many scattered bundles are seen in the olfactory striatum.

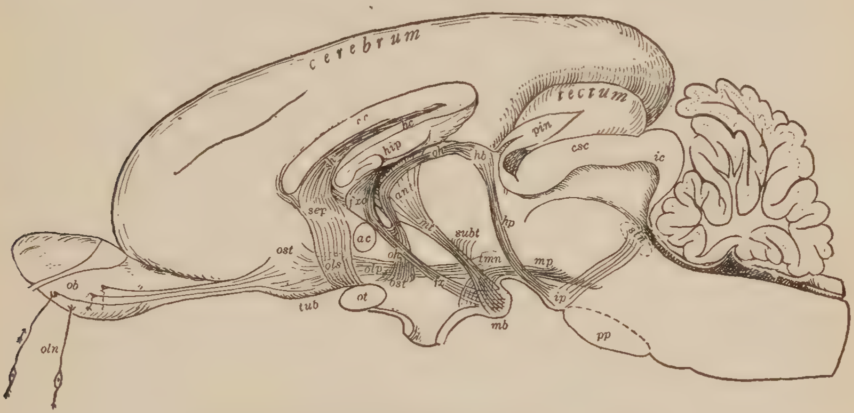

FIG. 175. The medial olfactory tracts of a rabbit.

In the dorsal border of the caudate nucleus (*cdn*) note the large **subcallosal bundle** (*ct*, the fibers *fnc* of Dejerine). It extends over the outer surface of the nucleus and underlies the corpus callosum. The origin of this tract is uncertain but its fibers have been shown to come from the region of the occipital cortex. According to some authors they come from the septal region. Traced backwards the subcallosal bundle (*ct*) appears to join the terminal stria (*tst*). In the caudate and putamen note the many scattered bundles that converge on the internal capsule. Fibers that pass down in the medial border of the cerebral peduncle form the **olfacto-peduncular tract** (*olp*) which is homologous with the strio-thalamic or medial basal forebrain bundle of lower vertebrates.

At a lower level (fig. 177) the intimate relations of the striatum (*ost*) to the olfactory tubercle (*tub*) is more evident. This basal portion of the striatum which fills the interior of the olfactory tubercle is greatly developed in all macrosmatic mammals and gives origin to the olfacto-peduncular tract (*olp*). The olfactory tubercle also gives rise to a band of **olfacto-septal tracts** (*ols*) which are seen passing dorsally in the sub-callosal gyrus (32) to reach the septal nuclei (*sep*). The septo-hippocampal tract (*sh*) or fornix longus is seen taking origin in the septal region (*sep*) and passing backwards under the corpus callosum (*cc*) to join the hippocampal commissure and angular bundle.

The temporal division of the anterior commissure (*ac*) passes laterally and separates the basal **motor olfactory striatum** (*ost*) from the caudate nucleus and putamen. It sweeps over the external surface of the putamen forming the external capsule (*e*). This fiber layer is augmented by many fibers that arise in the lateral olfactory nuclei in the piriform area (*pir*). Covering the lateral surface of the external capsule (*e*) is the nucleus called the claustrum (*clau*). It should be noted that the lateral olfactory tract (*lot*) is ending over the surface of the piriform area (*pir*). The **terminal stria** (*tst*) is a band of fibers seen passing in the medial side of the caudate nucleus just in front of the anterior nucleus of the thalamus. The terminal stria makes connections with the olfactory striatum.

In a lower section (fig. 172) the **anterior commissure** (*ac*) is seen crossing below the septal region. Its two portions stain differently. Figure 184 shows the connections of the two components of this commissure. The darkly staining ventral fibers are *U*-shaped and connect the two olfactory bulbs. They form the true olfactory commissure. The lighter staining dorsal part connects the olfactory area with the opposite putamen (*put*), lateral olfactory nuclei (*lon*), claustrum (*clau*) and amygdala (*amy*). Over the lateral surface of the putamen its fibers form a thin layer, the **external capsule** (*e*). Many fibers from the lateral olfactory nucleus (*lon*) also pass dorsally into the external capsule (*e*) and the claustrum also contributes fibers to the anterior commissure. The columna of the fornix (*fx*) are seen curving down over the anterior commissure. On each side they are joined by the olfacto-habenular tract (*oh*). The dorsal (*dor*) and anterior (*ant*) nuclei of the thalamus are seen medial to the internal capsule (*int*). The motor olfactory striatum (*ost*) is here dispersed in the cerebral peduncles and takes the name of peduncular nucleus. Note how the ventral surface of the nucleus is invaded and intimately connected with the deep fibro-cellular layers (*fcl*) of the olfactory tubercle (*tub*). On the surface is recognized the olfactory cortex (*tub*). Deep to this is a thick fibro-cellular layer (*fcl*), containing in its lateral part a lateral olfactory nucleus (*lon*). The lateral olfactory nucleus (*lon*) contributes fibers dorsally into the external capsule (*e*). More medially the olfacto-septal tracts (*ols*) are seen. The deepest layer is formed by the olfacto-peduncular tracts. These are seen as scattered fiber bundles

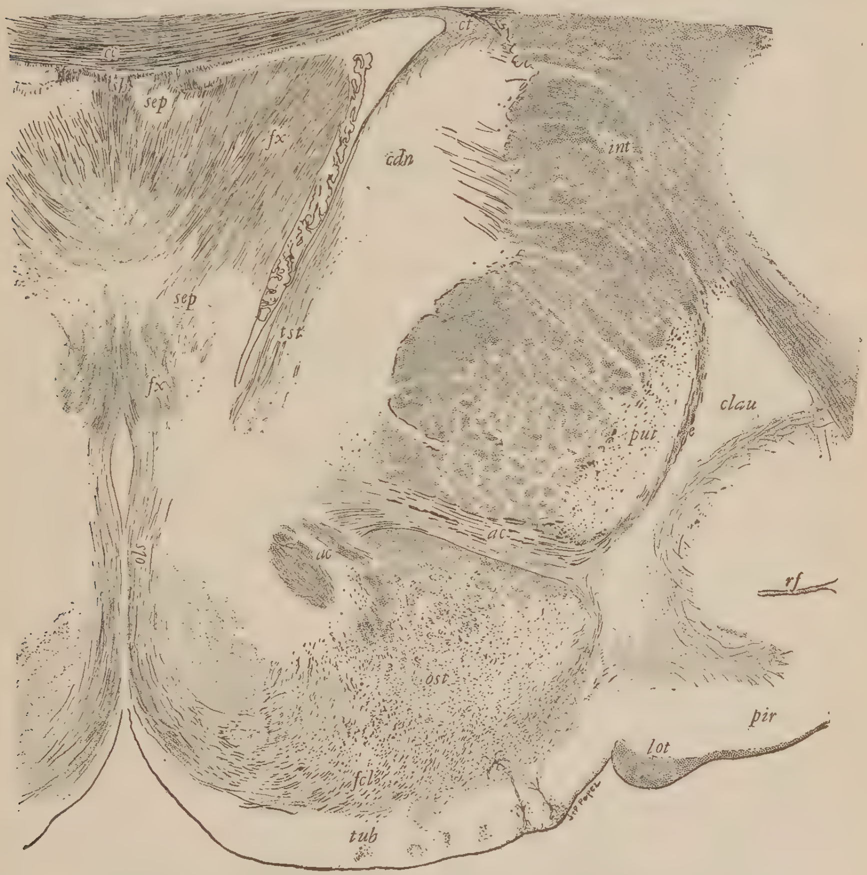

FIG. 176. Section through the olfactory tubercle, cat, × 7½.

that arise from cells in the motor olfactory striatum or peduncular nucleus (*ost*) and pass down in the medial border of the cerebral peduncles to end in the tubero-mammillary nucleus (*tmn*).

Traced downwards through sections (figs. 172 to 169) the olfactory striatum is seen to give rise to the olfacto-habenular tracts (*oh*). Here the motor olfactory striatum (*ost*) invades the peduncles and

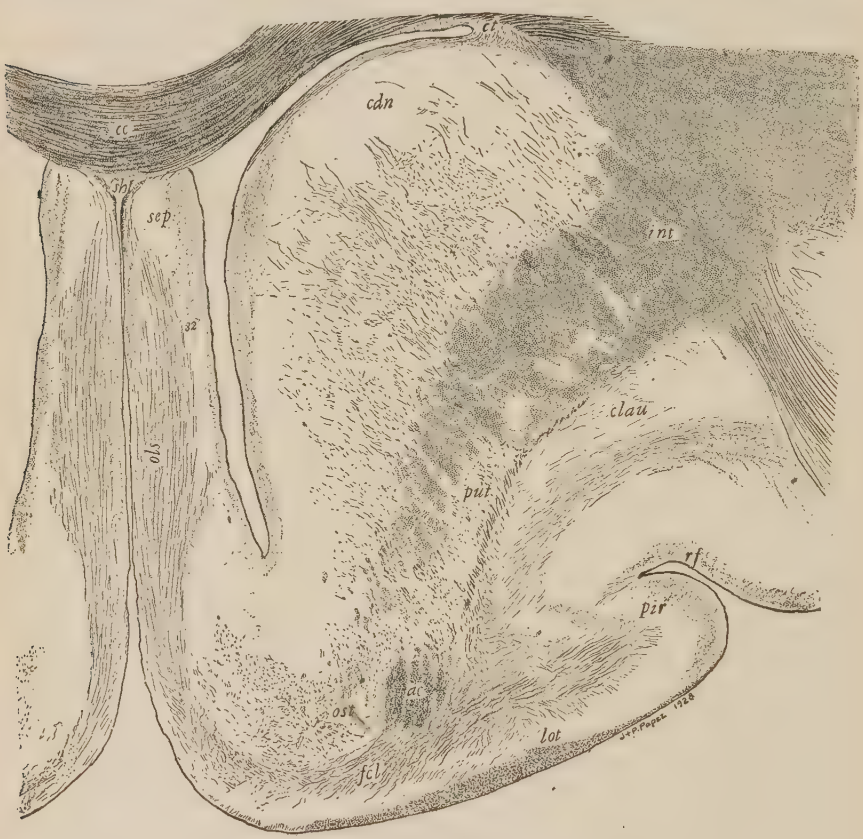

FIG. 177. Section through the front of olfactory tubercle, cat, × 7½.

is known as the peduncular nucleus at the level of the chiasma. By its position it can be readily distinguished from the globus pallidus. As the optic chiasma is approached the olfactory striatum is enclosed in the peduncle, becomes reduced in size and soon disappears.

The lower motor striatum

The lower motor striatum is formed by the lentiform nucleus which consists of the putamen (*put*) and globus pallidus. These are seen to separate from the olfactory striatum in figure 171. At lower levels (fig. 170) separation becomes complete. The putamen is situated lateral to the internal capsule (*int*) and between them is now seen its motor center, the globus pallidus (*gp*). The **globus pallidus** (*gp*) appears as a layer of fibers and cells lateral to the motor olfactory striatum or peduncular nucleus (*ost*). The globus pallidus (*gp*) is a motor center related to the putamen. It is quite independent of the motor olfactory striatum (*ost*). The commissure of Meynert (*mc*) connects the globus pallidus dorsal to the chiasma with the globus pallidus of the other side. From the globus pallidus, the **strio-peduncular fibers** (*stp*) stream medially into the peduncles. Some pass ventral to the peduncles (fig. 169), turn around their medial border and form the ansa lenticularis (*ansa*) which passes to the tubero-mammillary nucleus (*tmn*) and downwards to the oculomotor, ciliary and interstitial nuclei.

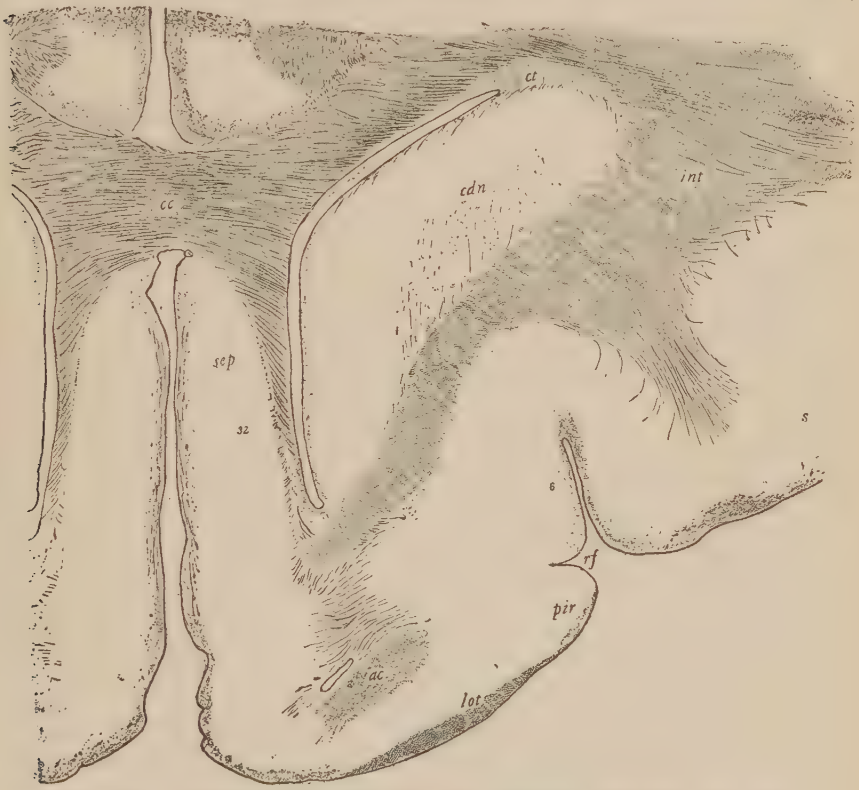

FIG. 178. Section through the base of the olfactory peduncle, cat, × 7½.

At this level (fig. 169) the putamen receives the thalamic fasciculus (*tf*) from the reticular subthalamic nucleus (*sub*). Adjacent to the mammillo-thalamic tract (*mt*) is the special part of the reticular subthalamic nucleus (*sub*) in which the lateral division of the mammillo-thalamic fasciculus (*mt*) ends. The anterior part of the thalamic fasciculus (*tf*) arises from this nucleus. Thus it is possible that the excitations that arise in the mammillary bodies are conducted to the upper end of the putamen and probably also to the caudate nucleus by the anterior part of this fasciculus.

The ventral border of the putamen (*put*) and the lateral olfactory nucleus (*lon*) join the **amygdala** (*amy*) within the **piriform area** (*pir*). Within this is seen ending the posterior division of the anterior commissure (*ac*) augmented by some other fibers. At lower levels (fig. 169) the **terminal stria** (*tst*) is seen to arise from the medial side of the amygdala and pass dorsally along the side of the optic tracts. The stria can be traced dorsally along with the tail of the caudate nucleus (*cdn*) over the internal capsule along the lateral border of the thalamus to end in the olfactory striatum in the region of the olfactory tubercle (fig. 177, *tst*).

In sections through the tuber cinereum (fig. 168) fibers of striatal origin are seen on both sides of the cerebral peduncles (*ansa*, *stp.*). Many others pass through the lateral border of the peduncles into the subthalamic region to enter the peripeduncular (*peri*) and subthalamic (*snl*) nuclei. Here the main part of the reticular subthalamic nucleus (*sub*) is very large and receives the terminal fibers of the brachium conjunctivum (*bc*) on its medial side. A loose stream of fibers, the thalamic fasciculus (*tf*) arises from this nucleus and passes laterally to join the internal capsule (*int*) through which it passes to the putamen at higher levels.

In sections in front of the red nucleus (fig. 167) the thalamic terminus of the brachium conjunctivum (*bc*) ends in the reticular subthalamic nucleus (*sub*). From this the thalamic fasciculus (*tf*) takes origin and extends to the internal capsule (*int*) to pass up to the putamen. Motor excitations of cerebellar origin thus reach the putamen. Fibers from the putamen pass into the globus pallidus. From this the strio-peduncular tracts (*stp*) and ansa lenticularis (*ansa*) pass down in the peripeduncular region. These striatal fibers end in the subthalamic (*snl*), peripeduncular (*peri*), tubero-mammillary (*tmn*), intrapeduncular, tegmental (*teg*), ciliary (*cil*), interstitial (*is*), oculomotor (*om*), masticator (*mn*) and facial (*fn*) nuclei.

The histological structure of the corpus striatum is also very characteristic and primitive. The caudate and putamen are composed of tubular clusters of large quantities of **small** radiating cells with short axis cylinders. Among these cells the incoming or afferent fibers of the subcallosal tract (*ct*) and the thalamic fasciculus (*tf*) branch and end. Within these clusters appear **large** branching cells which send their long axis cylinders into the small fiber bundles that are so characteristic of these nuclei. These fibers end in the motor olfactory striatum or in the globus pallidus. Both of these centers serve as motor centers of the striatum. Their large motor cells give

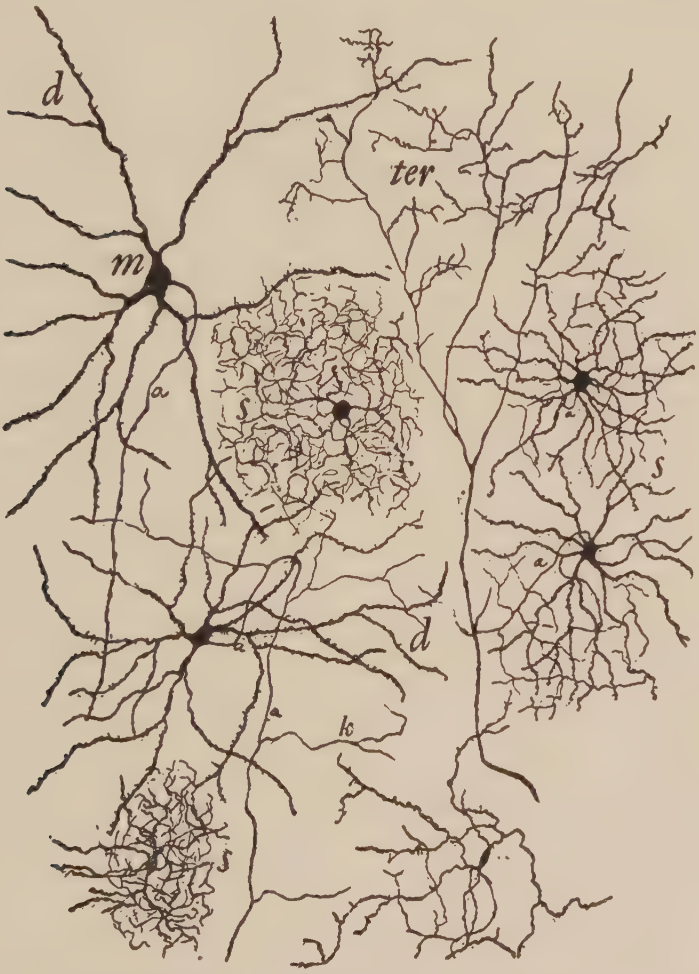

FIG. 179. Section showing cell structure of the striate body. From Cajal.

rise to fibers that pass through and around the peduncles as the olfacto-peduncular, strio-subthalamic, strio-peduncular and strio-bulbar tracts (fig. 179).

Theory of function of the striate body

The striatum may be regarded as a very primitive form of cortex derived from the olfactory centers. Its structure and connections suggest that it is composed of a large series of motor valves for releasing various groups of purposive movements commonly called instinctive responses. Its integrity is necessary for the performance of these associated, purposive and stereotyped reactions. The purposes of these movements may be various. They may provide for securing, selecting or rejecting of food; for chewing, swallowing, nursing, laughing, crying, facial expression, or for eye and head movements, for walking, prehension, etc. It is thus a very primitive but essential mechanism for directing movements into the appropriate channels of response. For its normal functioning it requires intact spinal, spino-cerebellar and cerebello-spinal as well as cerebello-mesencephalic motor reflex mechanisms in connection with which its valve-like action is exercised.

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CHAPTER 31

STRUCTURE OF THE OLFACTORY BRAIN

A PLAN of the chief olfactory connections is seen in figures 175 and 181. The olfactory brain consists of eight parts: (1) the olfactory mucous membrane which gives rise to the olfactory nerves (*oln*); (2) the olfactory bulb (*ob*) in which the olfactory nerves end and from which the olfactory tracts (*lot*) and the olfactory part of the anterior commissure (*ac*) take their origin; (3) the ventral olfactory area (triangle, tubercle, anterior perforated area and the septal area) in which the medial olfactory tracts end, and which make connections through the olfacto-septal tract (*ols*) with the septum (*sep*) and hippocampal formation (*hip*), with the habenular nuclei (*hb*) and tuber cinereum (*tc*); (4) the motor olfactory striatum (*ost*) which receives fibers (*ols*) from the ventral olfactory area, heads of caudate and putamen and the terminal stria (*tst*) from the amygdala, and emits the olfacto-peduncular (*olp*) and olfacto-habenular (*oh*) tracts; (5) the piriform area (*pir*) in which the lateral olfactory tract (*lot*) ends and from which the piriform hippocampal tract or angular bundle (*ang*) arises that ends in the dentate gyrus of the hippocampus; (6) the hippocampal formation which emits the fornix (*fx*) which in turn ends in the mammillary nuclei (*mb*); (7) the mammillary bodies (*mb*) which emit the mammillo-thalamic tract (*mt*) to the anterior nucleus of the thalamus and to the anterior part of the reticular subthalamic nucleus (*subt*) of the thalamus; (8) the head of the caudate (*cdn*) and putamen (*put*) and the amygdala (*amy*) may be included here; for they appear to receive the fibers of the anterior commissure and connect with the motor olfactory striatum.

The **olfactory mucous membrane** in all macrosmatic mammals is found to be a moist surface greatly expanded over an elaborate system of turbinated processes within the nose (fig. 180). These are incompletely developed in Birds and Reptiles and reduced in the microsmatic aquatic Mammals and in most Primates. The olfactory mucous membrane, spread over these processes, contains the olfactory hair cells which are excited by odorous substances in solution on the moist surface. From these hair cells arise the non-myelinated olfactory nerve fibers (fig. 181). These pass through the cribriform plate of the ethmoid bone and end by dense tufts in the glomeruli of the olfactory bulb.

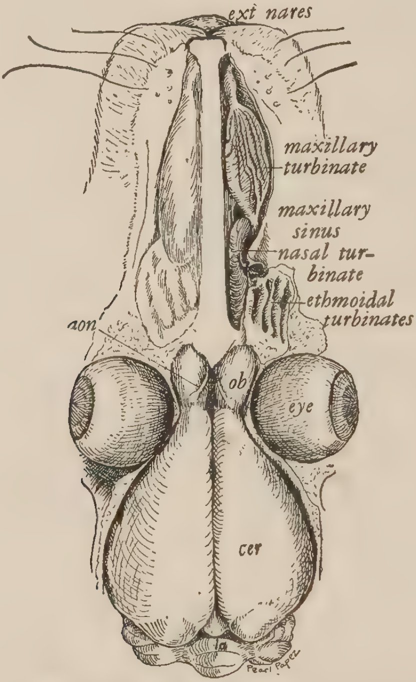

FIG. 180. The nasal capsules and olfactory bulbs of a rabbit, × 1.

The **olfactory bulb** (fig. 182) consists of seven layers:

1. The outer layer of olfactory nerve fibers.
2. The layer of olfactory glomeruli and outer granule cells.
3. The outer plexiform layer of fibers and small mitral cells.
4. The layer of mitral cells and middle granule cells.
5. The inner plexiform layer of fibers.
6. The inner granular layer.
7. The white substance.

From silver preparations Cajal has shown the following relations of these layers (fig. 183). The olfactory nerve fibers enter the first layer and end by means of tufts in the glomeruli (*gl*) of the second layer. The small mitral cells of the third layer, as well as the large mitral cells of the fourth layer, send stout dendrites that arborize in the glomeruli (*gl*). The axones (*a*) of the mitral cells pass into the sixth layer and enter the white substance; there some form the fibers of the olfactory tracts (fig. 182, *lot*) and others become fibers of the anterior commissure (*ac*). The granule cells (*g*) around the glomeruli in the second layer send their dendrites into the neighboring glomeruli while their axones extend over and end in other glomeruli, thus uniting them in larger groups. The cells of the middle and inner granular layers (6) send their branches transversely through all the layers. The outer plexiform layer (3) consists of branches of these granule cells, dendrites of the mitral cells and collaterals (*k*) from their axones. Most of the small mitral cells are in this layer. The inner plexiform layer (5) is a narrow zone formed by collaterals (*k*) of the small mitral cells and incoming fibers of the anterior commissure coming from the olfactory bulb of the other side. These probably end on the granule cells.

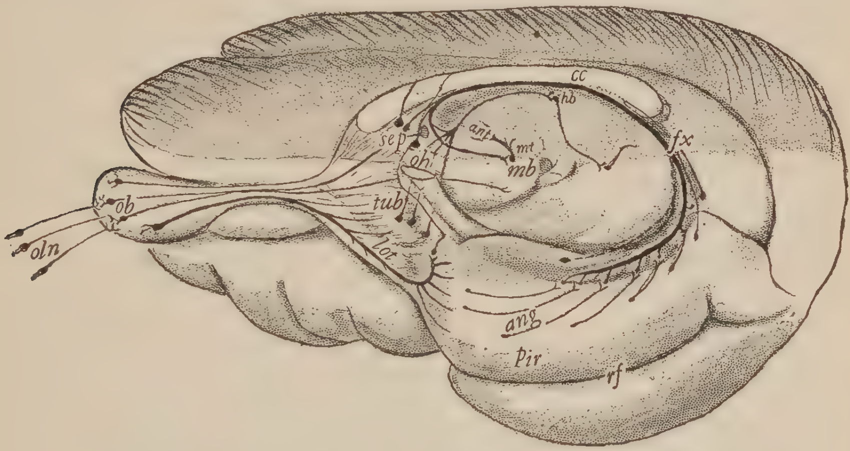

Fig. 181. Olfactory connections projected on the surface of hemicerebrum of a cat, × 2.

In the dorsal side of the olfactory bulb (fig. 180) is the small **accessory olfactory bulb** in which ends the accessory olfactory nerve (*aon*) from the vomero-nasal organ. The cells are small and the whole structure appears to be rudimentary, resembling the olfactory bulb of lower vertebrates. Small triangular cells are recognized which appear to have connections resembling the mitral cells of the main bulb. The glomeruli are rudimentary. The cells give rise to fibers that enter the olfactory tracts.

The **olfactory peduncle** (fig. 182) is a cylindrical stalk that connects the olfactory bulb with the olfactory triangle and the olfactory tubercle. The glomeruli and mitral cells are absent. The smaller granular polymorphous cells form a rudimentary cortex, the anterior olfactory nucleus. The fibers of the sixth layer of the bulb separate into two general bands; the olfactory tracts (*lot*) which become external, and the anterior commissure (*ac*) which remains internal close to the center.

Two **olfactory tracts** (*lot*) are formed by the long axones of the larger mitral cells. As they pass along the peduncle they give off collaterals that arborize among the terminals of the granule cells, which in turn send their axones into the anterior commissure. The **medial olfactory tract** (*mot*) fibers end in the cortex of the olfactory trigone and tubercle which covers the surface of the motor olfactory striatum. The fibers of the **lateral olfactory tract** (fig. 184, *lot*) are prolonged backwards to end in the cortex of the piriform lobe (*pir*), into which they radiate a great quantity of collaterals all along their course.

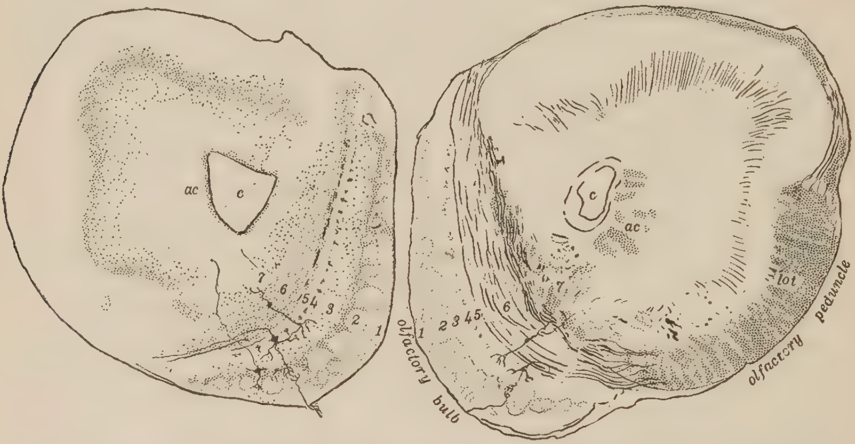

Fig. 182. Sections of olfactory bulbs of the opossum, through their posterior part. Left, cell stain. Right, fiber stain, × 12.

The **anterior commissure** (fig. 184, *ac*) consists of fibers derived from the smaller mitral or tuft cells of both sides. They pass along the center of the peduncle, decussate in the terminal lamina and enter the olfactory bulb of the other side as well as the lateral olfactory nucleus (*lon*), claustrum and amygdala (*amy*). Its two parts become evident. The ventral part forms the *U*-shaped olfactory commissure which connects one bulb with the other. The dorsal part passes laterally through the striatum and divides into a descending limb to the amygdala (*amy*) and a dorsal limb that spreads over

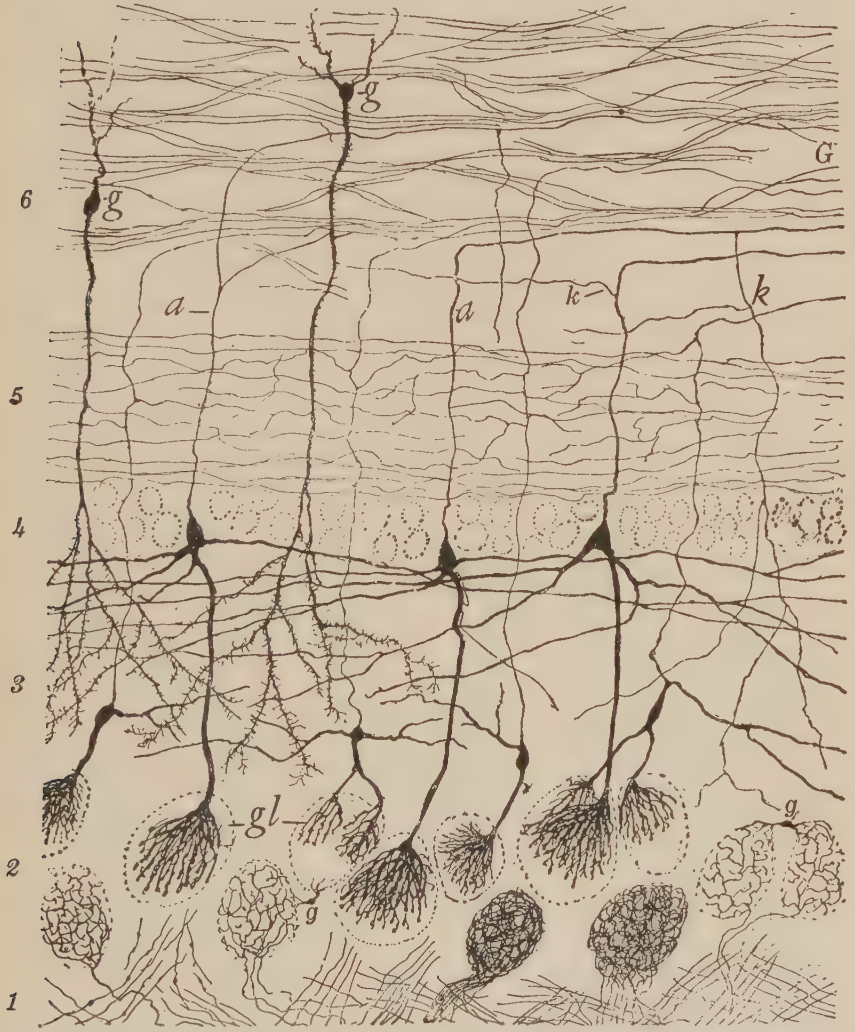

FIG. 183. Cell structure of the olfactory bulb. Silver cell stain. Golgi method. From Cajal.

the outer surface of the putamen in the external capsule (*e*). Its fibers appear to end in the putamen and caudate, and send collaterals into the claustrum and insular cortex. Most authors state that this part of the anterior commissure is distributed to the temporal and piriform cortices. From the distribution of the anterior commissure it seems that the olfactory bulb of one side discharges excitations into the olfactory bulb, the lateral olfactory nucleus, claustrum and the amygdala of the other side.

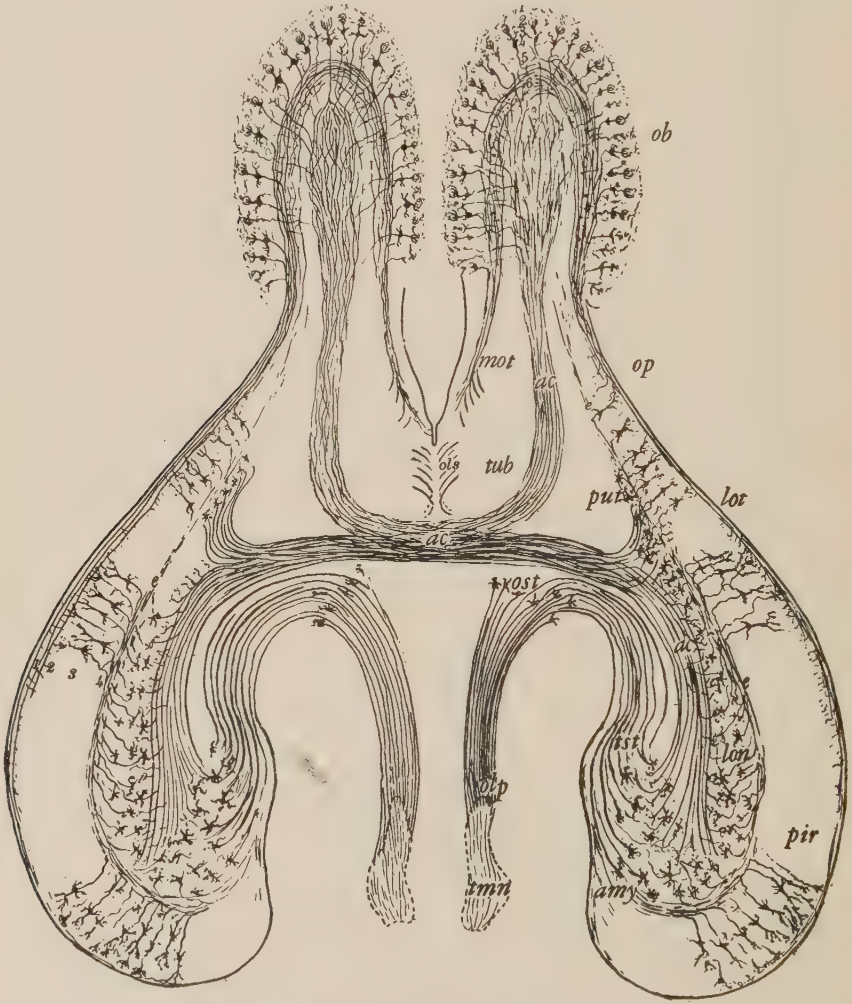

FIG. 184. A plan of the cells of origin and the fiber connections of the anterior commissure.

The **ventral olfactory** area includes the cortex of the **olfactory triangle, tubercle** (anterior perforated area), and the diagonal band. In this rudimentary cortex the medial olfactory tracts are dispersed, and their fibers end here. This area consists of (1) an outer plexiform layer in which the olfactory tract fibers arborize; (2) a layer of medium-sized pyramidal cells in which many cell clusters, or islands of Calleja, occur; and (3) a very thick layer (*fcl*) of polymorphous cells interspersed with myelinated fibers. This third layer forms the large fibrocellular layer that sends the olfacto-septal fibers (*ols*) along the subcallosal gyrus into the septum and to the hippocampal rudiment which overlies the corpus callosum. Another small tract passes down to end in the lateral nucleus of the tuber cinereum. Laterally is the small **lateral olfactory nucleus** (*lon*) that sends its fibers dorsally into the external capsule (*e*) to the putamen.

The **motor olfactory striatum** (*ost*) is formed by the union of the heads of the caudate and lentiform nuclei ventral to the anterior commissure. The third layer (*fcl*) of the ventral olfactory area is quite intermixed with the striatum (*ost*) and it is from this junctional region that the **olfacto-peduncular tracts** (*olp*) are projected downwards in the medial border of the cerebral peduncles and the olfacto-habenular tracts (*oh*) dorsally to the habenular body (*hb*). In the macrosmatic mammals the third layer and the olfactory striatum are very large, giving rise to the prominence called the **olfactory tubercle.** From these connections it appears that the cortex of the olfactory tubercle receives olfactory excitations from the bulb. It then redistributes them to the olfactory striatum. From the olfactory striatum tracts pass to the habenular nuclei, to the tuberomammillary nucleus and other nuclei along the medial side of the cerebral peduncles. This is probably a primitive system of connections since similar fiber connections are found in the lower vertebrates.

The **piriform area** (*pir*) has a more typical cortical structure than the ventral olfactory area (fig. 185). It consists of six layers. (1) The **lateral olfactory tract** (*lot*) spreads over its surface as a fiber layer (*F*) and sends into it a great quantity of collaterals (*k*) which form an outer plexiform layer (*M*). (2) A layer of stellate-shaped granule cells (*G*) whose branching dendrites are embedded in the plexiform layer. (3) A layer of pyramidal cells (*P*) of medium size. (4) A layer of nerve fibers and polymorphic cells (*S*). (5) A layer of white substance which the axones (*a*) of the pyramidal cells (*P*) enter. As they enter they bifurcate (*bf*). Polymorphic cells whose axones (*a*) pass to enter the sixth layer. (6) A layer of white fibers which separate the piriform cortex from the claustrum, putamen and amygdala (*amy*). This band of fibers passes dorsally as the angular bundle (*ang*) and hippocampal commissure (*hc*).

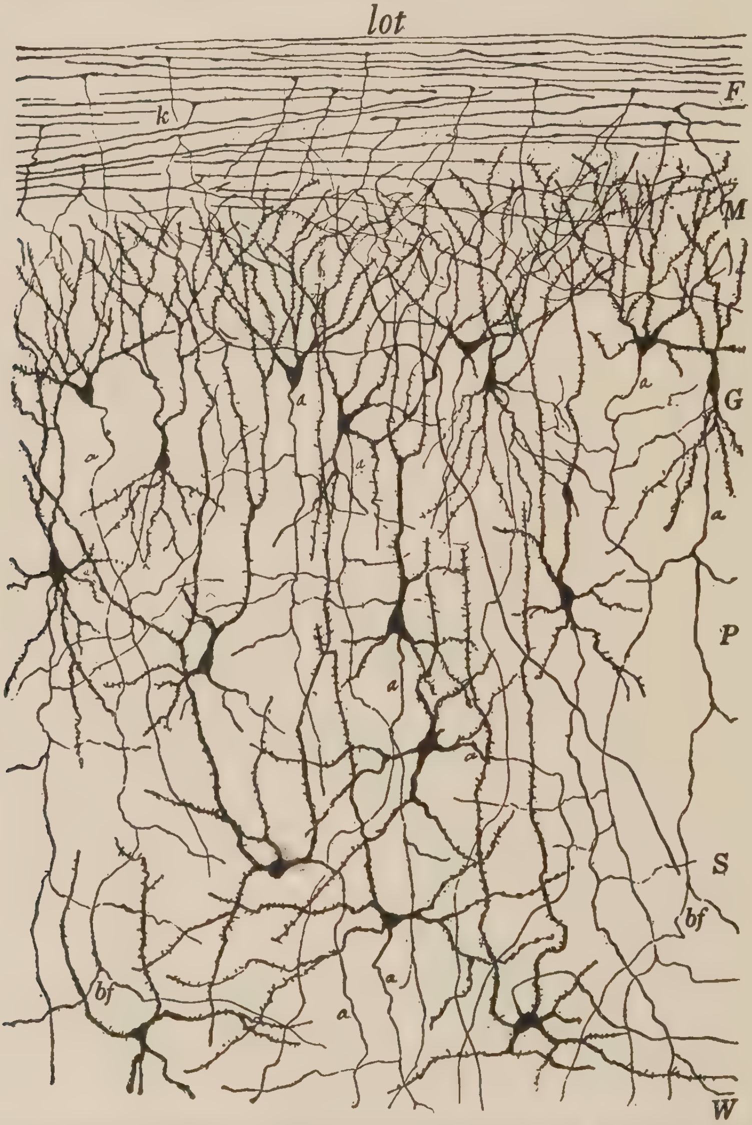

FIG. 185. Section through the piriform area of a rabbit. Golgi method. From Cajal.

The piriform area is continued backwards as the hippocampal gyrus or superior temporal nucleus of Cajal which is more densely fibrous. But the medial border that joins the hippocampus has a modified structure and is known as the subiculus (*sb*).

According to Cajal the fibers of the stellate and pyramidal cells that form the deep layer (6) form the **angular bundle**. It passes in the medial wall of the ventricle along the angle formed by the hippocampus and wall of the cerebrum. A part of it penetrates the subiculum of the hippocampus as direct or perforating fibers and another part passes over its ventricular surface in the alveus and fimbria of the fornix to form the hippocampal commissure (*hc*) and end in the hippocampus of the other side. These direct (*ang*) and crossed (*hc*) piriform-hippocampal fibers may be seen in the inner ventricular angle where the hippocampus joins the piriform lobe opposite the subiculum. From the fiber connections it is evident that the piriform cortex receives olfactory excitations chiefly from the bulb of the same side through the lateral olfactory tract (*lot*). It seems also that fibers from some other source enter the deeper fourth layer of the piriform lobe; possibly they are commissural fibers or fibers of the anterior part of the piriform area. The piriform cortex is doubtless the region of olfactory sensations. The cells of this cortex form an extensive intercellular synaptic field which by means of the angular bundle discharges excitations into the hippocampal formations of both sides. It seems probable also that through the anterior commissure the piriform area is brought into functional relations with the amygdala, claustrum and the olfactory striatum.

The **amygdala** (*amy*) is a nuclear mass within the temporal tip of the piriform area (fig. 184). It is in continuity with the tail end of the caudate nucleus, the claustrum, the lateral olfactory nucleus and the ventral border of the putamen. From the putamen (*put*) these structures are in part separated by the external capsule (*e*) and the caudal extensions of the anterior commissure (*ac*). The commissure appears to be their chief afferent connection since its fibers are scattered within these nuclear masses. The amygdala consists of several nuclear masses. Its cells are small multipolar cells like those of the caudate. From the larger cells grouped on the medial side emerge the fibers of the **terminal stria** (fig. 186, *tst*). These curve over the internal capsule (*int*) with the caudate nucleus and enter the motor olfactory striatum ventral to the crossing of the anterior commissure (fig. 172). Some pass to the striatum of the other side by way of the anterior commissure. From its fiber connections the amygdala appears to be the caudal portion of the lateral olfactory nucleus. It receives olfactory excitations from the bulb through the anterior commissure and discharges these forward into the motor olfactory striatum, by means of the terminal stria. According to Cajal the strial fibers join and descend with the olfacto-peduncular tracts (fig. 186). The strio-peduncular tract (*stp*) arises from the adjacent striatum. It appears to be a center with subcortical olfactory connections like the anterior part of the caudate and lentiform nuclei. It may be looked upon as mediating some special stereotyped motor reaction. The connection of the temporal division of the anterior commissure with the putamen, caudate, claustrum and amygdala is mainly an olfactory one. Some authors state that the fibers of the temporal division of the anterior commissure are distributed to the overlying cortex of the temporal and piriform regions. Cajal states that a large number of the fibers in the temporal division of the anterior commissure come from cells of the anterior part of the piriform cortex.

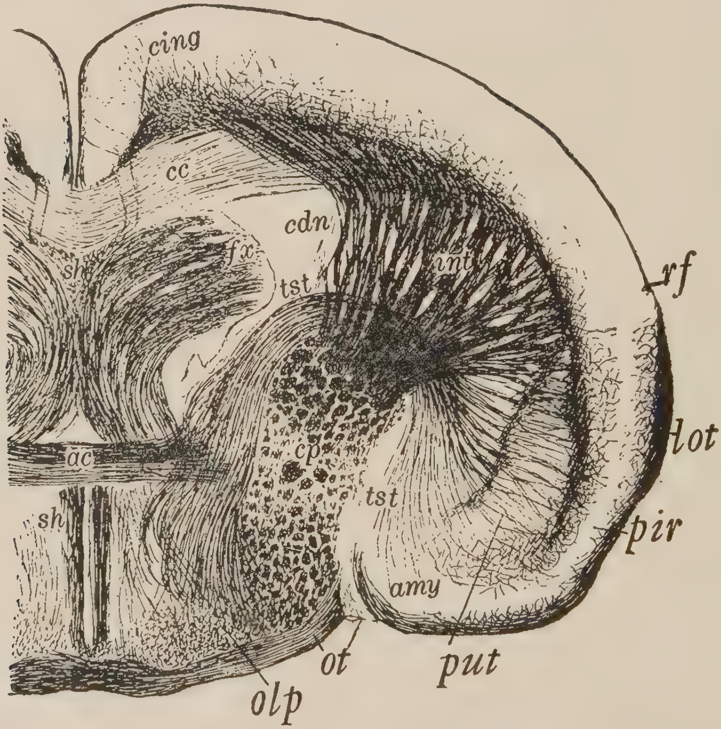

FIG. 186. Cross section through the piriform lobe and amygdala of a young mouse. From Cajal.

The **hippocampal formation** is divisible into three parts: (1) the hippocampal gyrus (104), the medial wall of which is called the subiculum (*sb*), (2) the hippocampus (*hip*) proper with the fornix fibers (*fx*) and (3) the dentate gyrus (96). The hippocampal gyrus (104) and dentate gyrus (96) can be seen in figures in the first seven chapters. The hippocampus (*hip*) is seen only on the ventricular surface of the brain (fig. 55).

The **hippocampal gyrus** (104) is a dorsal prolongation of the piriform area (*pir*), which it resembles in structure and functional connections. It is modified by its close relation to the hippocampus and its more distant relation to the lateral olfactory tracts. On account of the fact that here the stellate and pyramidal layers of cells have become condensed and infiltrated with great quantities of fibers from the more anterior part of the piriform area, Cajal has called it the superior temporal nucleus. Axones of these cells pass directly inward and around the margin of the ventricle where they join the angular bundle (*ang*). Fibers of the angular bundle take two courses. One group enters the subiculum as the perforating fibers (fig. 187, *perf*); the other group of fibers enters the alveus (6) of the hippocampus of the same side, joins the fornix, crosses in the hippocampal commissure (*hc*) and enters the hippocampus of the other side. It is this second group that forms the dorsal division of the hippocampal commissure (*hc*) in lower mammals while the anterior division of the commissure is formed by the fornix commissure in front of the thalamus (fig. 175, *fxc*). In brains of large size such as the higher Primates possess, the hippocampal gyrus is elongated; and the perforating fibers (*perf*) from the inner surface of the piriform lobe pierce the subiculum and appear upon its medial side as a superficial fiber stratum of the **subiculum.** These fibers extend in an upward direction and enter the hippocampal fissure to end in the lacunar layer (2).

The hippocampus (*hip*) is an inturned gyrus which appears as a ridge on the ventricular surface. Its posterior border is continuous with the subiculum of the hippocampal gyrus. The following layers are recognized (fig. 187):

(1) An outer molecular layer that marks the line of fusion of the hippocampus with the dentate gyrus. The long dendrites (*d*) of the pyramidal cells (*p*) arborize in this and the next layer.

(2) The lacunar layer formed by the non-myelinated fiber terminals of the perforating fibers (*perf*) coming through the subiculum. According to Cajal fibers from the cingulum (*cing*) also enter the

lacunar layer through the upper end of the subiculum. Small stellate cells are dispersed in this layer.

(3) The radiating layer through which the long apical dendrites (*d*) of the pyramidal cells (*p*) radiate to arborize in the lacunar (2) and molecular layers (1). Among the branches of these apical dendrites end the axones of the granule cells (*G*) of the dentate gyrus. Aberrant stellate cells occur here.

(4) The pyramidal cell layer, many cells deep. Each pyramidal cell (*p*) sends a stout apical dendrite (*d*) through the radiating layers (3) to arborize in the lacunar (2) and molecular layers (1). Their basal dendrites arborize in the fifth layer. Their axones pass into the fornix and give off a collateral (*k*) back into the radiating layer (3).

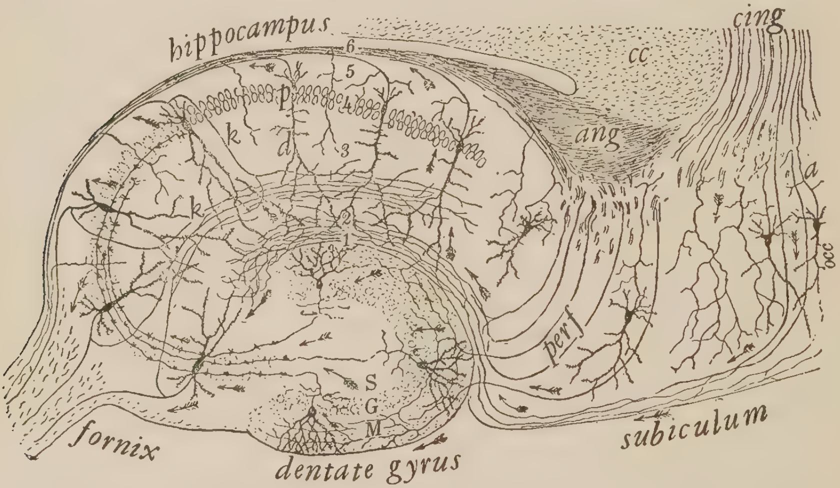

Fig. 187. A schema of the structure and connections of the hippocampal formation. Golgi method. From Cajal.

(5) A layer of polymorphous cells among which arborize the basal dendrites of the pyramidal cells as well as the crossed fibers (*a*) of the angular bundle that enter the alveus from the fornix. They come from the hippocampal commissure. Some of these polymorphous cells send their axones into the lacunar layer (2), while others send them into the pyramidal layer (4) where they arborize on many cells reminding one of the basket cells of the cerebellum.

(6) The alveus is the layer of white fibers that covers the ventricular surface of the hippocampus. It consists of efferent fibers from the pyramidal cells that pass forward to form the fornix, and of

afferent fibers (*ang*) from the piriform lobe of the opposite side that cross through the hippocampal commissure and pass back by way of the fornix to end in the hippocampus.

The **dentate gyrus** (96) appears as a wrinkled strip of cortex between the fornix (*fx*) and the hippocampal gyrus (104) enclosed in the concavity of the hippocampus. Like the hippocampus it is a modified piece of cortex consisting of the following layers: (*M*) The molecular layer in which enter the septo-hippocampal fibers (*sh*) and fibers from the hippocampal rudiment (fig. 175); (*G*) a thick layer of granule cells whose dendrites branch into the molecular layer and whose axones give a number of collaterals into the deeper layer of polymorphous cells and then pass into the radiating layer (3) of the hippocampus to end in peculiar thickenings on the apical dendrites (*d*) of the pyramidal cells; (*S*) a layer of polymorphic or stellate cells among which end collaterals of the axones of the granule cells as they pass through this layer. The axones of the polymorphic cells pass into the fornix. The fornix (*fx*) is formed by the axones of the pyramidal cells (*p*) of the hippocampus. It passes forward over the thalamus with the fibers of the angular bundle which form the dorsal hippocampal commissure (fig. 175, *hc*). In front of the thalamus a part of the fornix fibers decussate forming the fornix commissure (*fxc*). At this point the fornix gives off a considerable number of fibers that join the olfacto-habenular tract (*oh*). Then the fornix descends to end in the lateral nucleus of the mammillary body (*mb*). From the medial nucleus of the mammillary body arises the mammillo-thalamic tract (*mt*) which ends in the anterior nucleus of the thalamus (*ant*) and in the anterior division of the reticular subthalamic nucleus of the thalamus (*subt*). Both of these nuclei connect laterally with the striatum. The olfactory tubercle (*tub*) connects with the septal nuclei (*sep*) by means of the olfacto-septal tract (*ols*). The septum is connected by the septo-hippocampal fibers (*sh*) probably with the dentate gyrus.

Theory of function of the hippocampus

The piriform area and hippocampal gyrus have the structure of a sensory cortex and are generally conceded to be the regions of olfactory sensation. In the hippocampus some of the typical cellular layers are suppressed and it appears to be chiefly emissive. It seems that the pyramidal cells are the chief emissive cells of the hippocampus, sending their excitations by the fornix fibers to the habenular and mammillary nuclei. The afferent excitations to these pyramidal cells have four sources: (*a*) from the piriform area and hippocampal gyrus as the angular perforating fibers, which end in the lacunar stratum, (*b*) from the polymorphic cells whose fibers also end in the lacunar stratum, probably receiving their excitations through the hippocampal commissure from the piriform area of the other side, (*c*) from cells that form extensive baskets around the pyramidal cells and combine these into larger functional groups, and (*d*) from the granule cells of the gyrus dentatus. The axones of the pyramidal cells give off collaterals which ramify in the layer of polymorphic cells and thus reinforce the tendency to group excitation. The afferent excitations that reach the branches of the granule cells in the molecular layer of the dentate gyrus are unknown, but it is quite possible that they are from the septo-hippocampal fibers (*sh*) from the septum and from the hippocampal rudiment which pass over the dorsal side of the corpus callosum. In this way the olfactory excitations from the medial and ventral olfactory cortex would reach the dentate gyrus while the excitations from the piriform lobe would reach the hippocampus. The fornix conducts hippocampal excitations to the nuclei of the mammillary bodies. Some of its fibers also join the olfacto-habenular tract to end in the habenular nuclei, which in turn discharge into the interpeduncular nucleus and that into the dorsal tegmental nuclei. The mammillo-thalamic tract conducts the impulses from the mammillary nuclei to the anterior nucleus of the thalamus. From this there appears to be a thalamo-cortical radiation into the uppermost portion of the internal capsule. Sach and Horsely state that this thalamic nucleus connects with the caudate; and it is possible that this is a mechanism for releasing or intensifying feeding or some other movements through the striatum. It is also important to note two other connections. The mammillo-thalamic tract gives off collaterals (Gudden's bundle) into the anterior part of the reticular subthalamic nucleus which in turn makes a striatal connection by means of the thalamic fasciculus. The mammillary peduncle which is to be suspected of conducting taste excitations also ends in the mammillary nuclei. Thus taste and smell may here combine to produce appropriate responses through the striatum.

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CHAPTER 32

Structure and Areas of the Cerebral Cortex

The **cerebral cortex** is the outer gray cellular layer of the cerebral hemispheres which everywhere covers the underlying white matter. In the smaller mammals (chapter 1) the cerebral cortex is smooth, but in the larger and higher forms it is folded out into sulci and gyri which cover corresponding laminae of white substance. Thus within the various higher orders such as the Ungulata, Carnivora and Primates, there arise characteristic groups of sulci and gyri which form a cerebral pattern typical for each group.

These gyrencephalic brains are an expression of growth and expansion of the cortex within a limited brain case. The factors most clearly evident in shaping the brain stem are also found operative in the productions of the cerebral patterns. Fiber systems, functional connections and the growth of the cellular areas with special adjustments are the determining factors. Around the base of the brain limitations are set by the base of the skull and by the primitive olfactory tracts and centers. The cortex is chiefly a dorsal expansion. In the lateral wall of the hemisphere passing through the striate body are the radiating fibers of the internal capsule. They form a central fan around which the cerebral cortex expands dorsally and radially. This group of thalamo-cortical radiations which first appear in the smooth brains of the lower mammals (fig. 188) is a primary factor in the developmental history of the cortical areas and the gyrencephalic patterns typical of the more advanced mammals. In the smooth brained mammal the internal capsule is seen to sweep into the deep layer of white substance of the hemisphere. The auditory radiations form a special plexus in the cortex of the temporal region (*ar*). The visual radiations invade the more dorsally lying occipital cortex (*or*). A similar group of unknown source invades the subiculum (*sb*); it appears to be related to the cingulum (*cing*). Another group of somatic radiations is distributed to the parietal and postcentral (coronal) regions. Projection fibers to the pons and motor nuclei arise from the frontal region around the cruciate gyrus (inferior precentral). The cellular structure of the cortex, at first more or less uniform, becomes altered by these invading fiber systems. Two types of cortical areas now appear; first, those invaded by the radiations and, second, the strips of cortex that separate them from each other, not invaded by the radiations. It is the first of these that can be looked upon as the **primitive functional areas** of the cortex, which undergo such rapid expansion under the stimulating influences of their thalamic or subcortical connections.

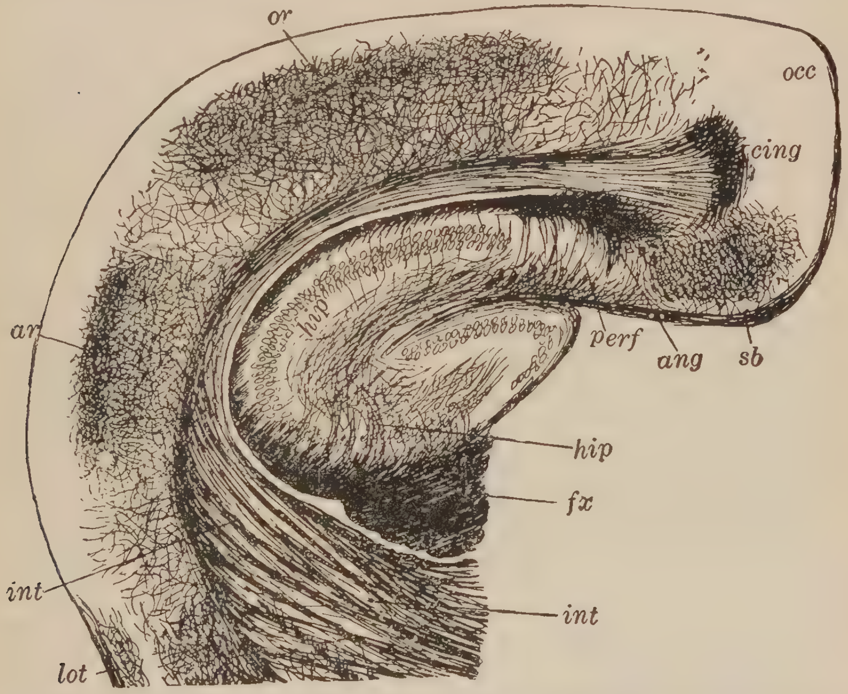


FIG. 188. Cross section of the left cerebrum of a mouse back of the corpus callosum. Golgi method. From Cajal.

A second factor is the less yielding expanse of the deep layer of white substance which in the smooth brains is quite uniform in thickness. In addition to the capsular fibers it contains great quantities of association fibers. As compared with the unyielding and inflexible nature of the white matter the cortex is a growing plastic tissue. As the primitive functional areas grow and expand they form gyri which draw away from the deep layer of white substance, but at the same time they acquire a central lamina of white substance through which their subcortical connections are retained.

Through the white substance the various sensory areas soon acquire intimate short connections with the surrounding neutral strips of cortex, and distant (long) connections, particularly with the frontal region which from the beginning appears to be the associative part of the cortex. In this way arise the **association tracts** of the cortex. The first long connection that becomes a distinct bundle is the **cingulum** (*cing*) which connects the medial side of the occipital cortex forward, with the medial frontal area bordering the cruciate gyrus. The operation of the foregoing factors is best seen in the brains of the lower orders and smaller forms. Thus in the spiny anteater (echidna) and the Marsupials it seems that the cerebral pattern is influenced chiefly by the radiations, expansions of the functional areas and antroposterior association fibers (fig. 2).

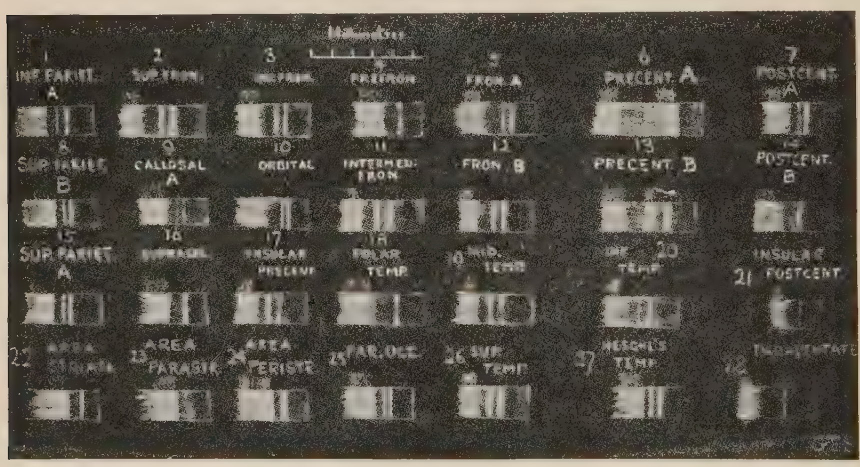
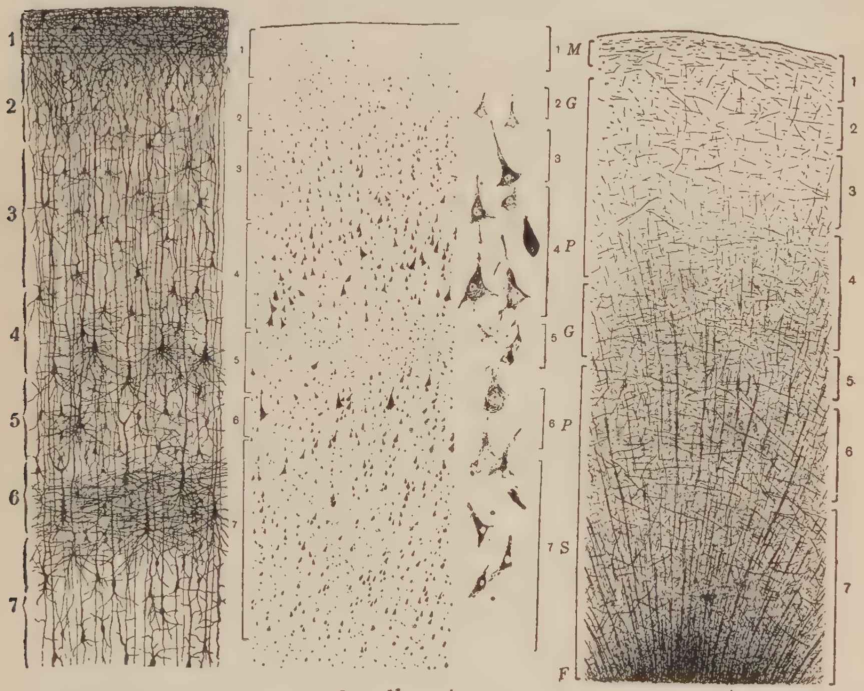


FIG. 189. Appearance of free-hand sections of the various areas of the human cerebral cortex. From G. E. Smith.

In the higher orders the **corpus callosum** becomes an additional factor whose influence is exerted in a transverse direction. Its fibers intersect those of the internal capsule and longitudinal association tracts of both sides and bind together the two hemispheres. In the larger Rodents, Edentata, Ungulata, Carnivora and Lemurs it tends to give a longitudinal direction to the sulci and gyri formed along the dorsal and medial border of the hemispheres. This influence is less marked in the higher Primates in whom the frontal lobe is large and the fronto-posterior association tracts are more prominent factors than in the Carnivora and Ungulata, and tend to offset the influence of the corpus callosum. In the higher orders, the walls of the cerebral hemispheres are very thick on account of the great quantity of the white matter formed by the nerve fibers that effect various kinds of connections with the nerve cells of the cerebral cortex.

The **cerebral cortex** in the human brain varies 2 to 4 mm. in thickness. A section of a fresh cortex shows that it is invaded by one or two thin **bands of white matter** which vary in position and density in different regions of the brain (fig. 189). Under the pia is a very thin superficial stratum. Thus the cortex is naturally divided into five or six layers. The deeper band is in some regions almost merged with the subcortical white matter which sends numerous **radial bundles** into the deeper layers of the cortex.



Golgi silver stain *Nissl cell stain* *Weigert fiber stain*

FIG. 190. Structure of postcentral gyrus of cerebral cortex. Silver stain from Cajal. Cell and fiber stain from Campbell.

The gray matter itself is a great expanse of nerve cells. They are of tall pyramidal shape and closely set in a forest-like formation, many layers deep. A typical cell (fig. 191) consists of a pyramidal cell body (*p*) containing a nucleus and a neurofibrillar network.

From the base of the cell many dendrites spread out and a long apical dendrite (*d*) runs to the surface to spread out in the superficial or molecular layer (*M*). From the base of the cell a slender axone (*a*) extends centrally to enter the white substance giving off one or more collaterals (*k*) on its way.

The number of **layers in the cerebral cortex** varies in different areas depending on the presence of one or more of the fiber bands or on the special development or suppression of one of the cell layers (fig. 190). The following layers are distinguished:

1. Outer molecular, zonal or plexiform layer (*M*) containing tangential nerve fibers and cells among which the apical dendrites of the pyramidal cells arborize.
2. External grandular layer of small pyramidal cells (*G*), whose apical dendrites arborize in the molecular layer and whose axones pass through the deeper layers to reach the white substance.
3. Layer of medium-sized typical pyramidal cells (*P*).
4. Layer of large pyramidal cells. Their basal dendrites arborize in the fiber network of the fifth layer. Many fibers enter and form dense pericellular networks (fig. 192) about the pyramidal cells. Their axones pass into the white substance.
5. Internal granular layer (*G*) containing small pyramidal and granule cells dispersed within the outer band of white substance formed by the sensory radiations.
6. Layer of large pyramidal cells whose basal dendrites arborize in relation to fiber network of the sixth layer. These large cells send their apical dendrites into the outer molecular layer. In the motor area these cells form the large pyramidal or motor cells of Betz. In the postcentral and precentral region similar but smaller cells probably give rise to the cerebro-pontal fibers. This is the important emissive layer of the cortex.
7. A layer of multiform or polymorphic cells dispersed by the nerve fiber bundles that are invading the cortex in great numbers from the underlying white substance.

Among the pyramidal cells of all the layers there are many smaller cells of less regular form (type II) with short complex axones branching among neighboring cells. The vast number of regular pyramidal cells send their axones in the **radial bundles** directly into the white matter (not into the bands). They become short association, long association, callosal or projection fibers which discharge their impulses into other regions of the brain.

Afferent fibers of various kinds reach the cortex from the white matter and enter into synaptic relations with its cells. They form two white **bands** which play an important part in subdividing the cortex into its layers (fig. 189). It seems likely that one (probably the outer) band may consist of the thalamic radiations while the other one consists of callosal or association fibers. These fibers form dense entanglements among the dendrites and bodies of the cortical cells, from which numerous button-like terminals end directly on the

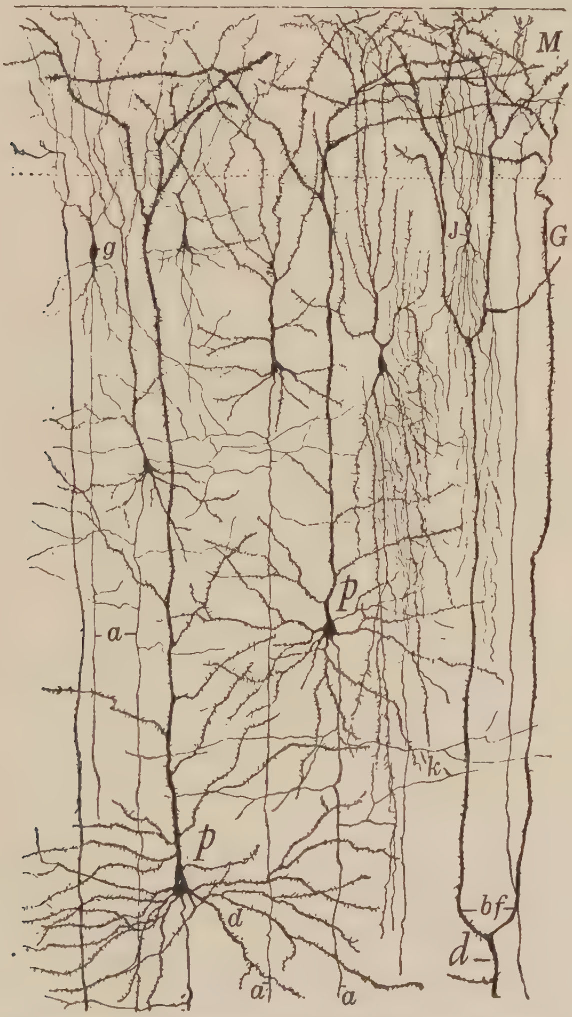


Fig. 191. A group of typical pyramidal cells of the cerebral cortex. From Cajal.

body of the cell (fig. 193). The many irregular spines and spurs upon the basal and apical dendrites are produced by such synaptic contacts of nonmyelinated fibers; but in the white bands and radiating bundles such contacts are not all synaptic, since these fibers are covered by a sheath of myelin. The superficial molecular or plexiform layer is also chiefly synaptic. Axones are seen to pass into these layers and end among the apical terminals of the pyramidal and external granular cells, reminding one of the molecular layer of the cerebellum. No doubt many of the terminal baskets around the pyramidal cells come from some of the granule, stellate and polymorphic cells which serve to combine them into functional groups. Another feature of this kind are the collaterals (*k*) which the axones of the pyramidal cells give off as they pass through the deeper cell layers. It is instructive to imagine how these vast numbers of brain cells with such intimate afferent, intercellular and efferent synaptic connections can serve the function of **irradiation** so highly developed in the cortex.

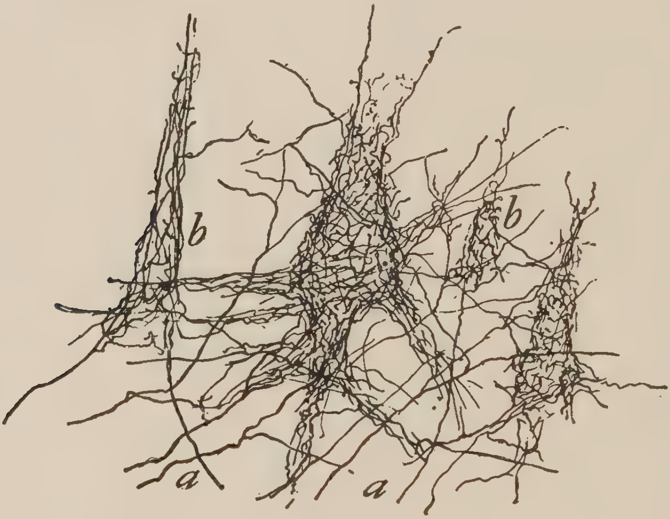


FIG. 192. Pericellular fiber plexuses around pyramidal cells of the cortex. From Cajal. Compare with figure 193.

The **original type of human cortex** consists of the six layers in which the three fiber layers, poor in cells, alternate with three layers, rich in pyramidal cells (fig. 194). From this type according to Brodmann all other secondary types are differentiated during fetal development. In many regions the original type is, therefore, transitory. The numerous secondary types that arise from it form nearly nine-tenths of the entire cortex of the adult human brain. They retain most of the features of the original six layers in modified form. The first or molecular layer and the sixth or multiform (polymorphic) layers are constant in all cortical regions of all mammals. In different regions of the cortex, one or more of the other layers may be reduced, enlarged or subdivided. On the basis of these differences the entire cortex has been mapped out into areas each of which is distinguished from contiguous areas by a difference in cell arrangement. A good example of this is shown by the striate and parastriate areas (fig. 194). In both, the original layers are recognized. In the striate area, the third is reduced and the fourth is enlarged and merged with the fifth in which the optic radiations form the dense outer white band of Baillarger. The sixth layer of large pyramidal cells is reduced and broken up by a great quantity of radiating fibers. In the parastriate area the third layer is broad and subdivided into two or three layers. The white band is faint and indistinctly double in the fifth layer.

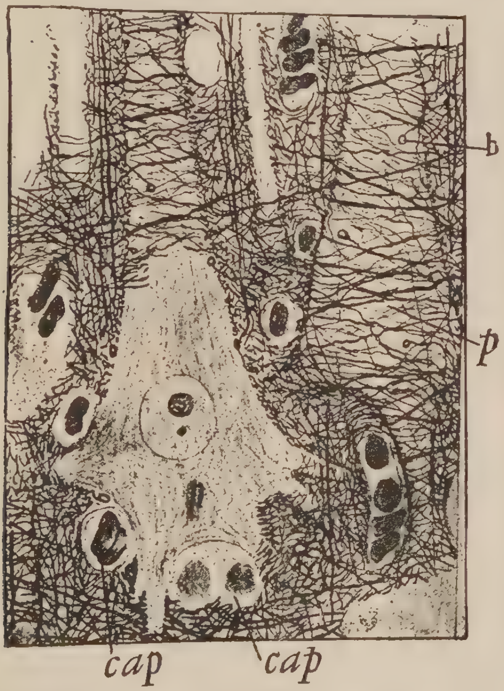


FIG. 193. Plexus of fiber terminals around pyramidal cells of the cerebral cortex of a dog. From Cajal.

The cortical areas of mammals

Nine main cortical regions, according to Brodmann, are recognized more or less clearly in the brains of all mammals. To these should be added the olfactory cortex and the hippocampus, making eleven in all:

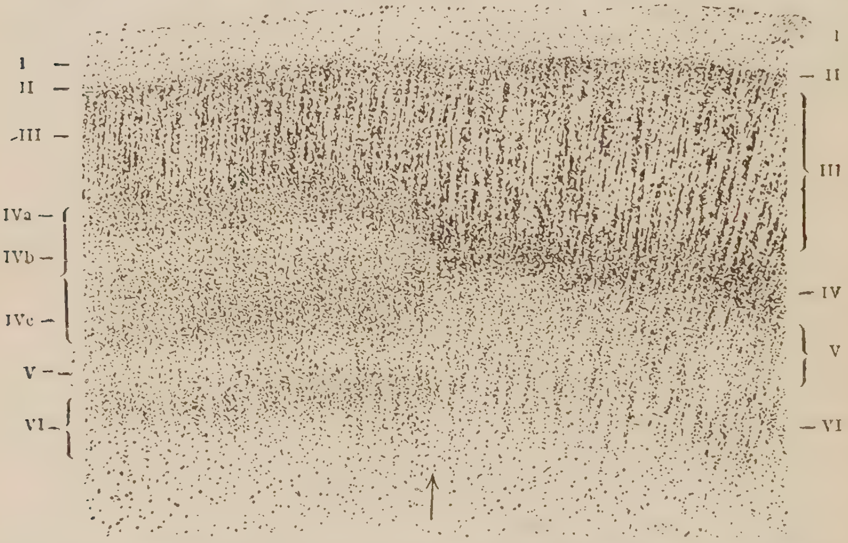
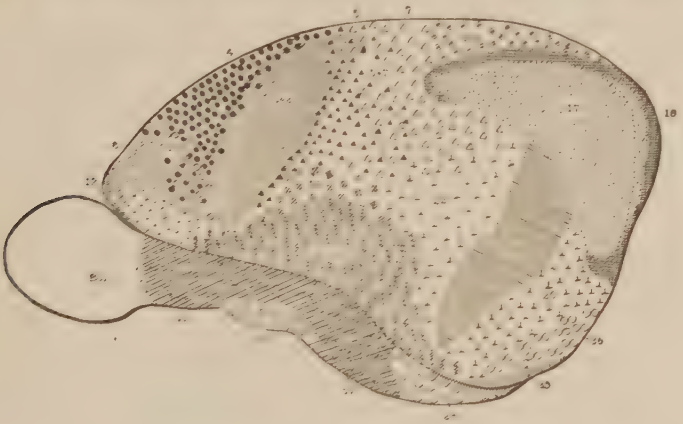
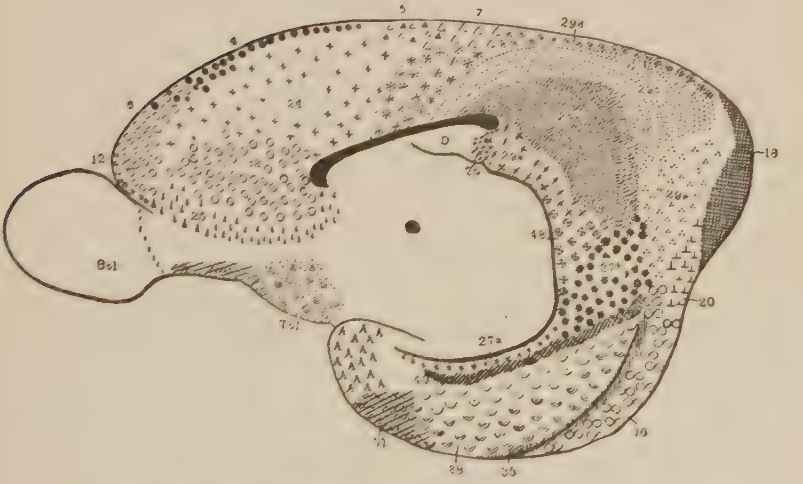


FIG. 194. Arrangement of cells in the cortex of the visual area (left) and the surrounding parastriate area (right). From Brodmann.

1. Post central region, deep sensory function
2. Precentral region, motor function
3. Frontal region, motor pattern function
4. Insular region
5. Parietal region, skin sensory function
6. Temporal region, auditory sensory function
7. Occipital region, visual sensory function
8. Cingular region (anterior part of limbic lobe)
9. Retrosplenial region (posterior part of limbic lobe)
10. Olfactory region, olfactory sensory function
11. Hippocampal formation, olfactory function

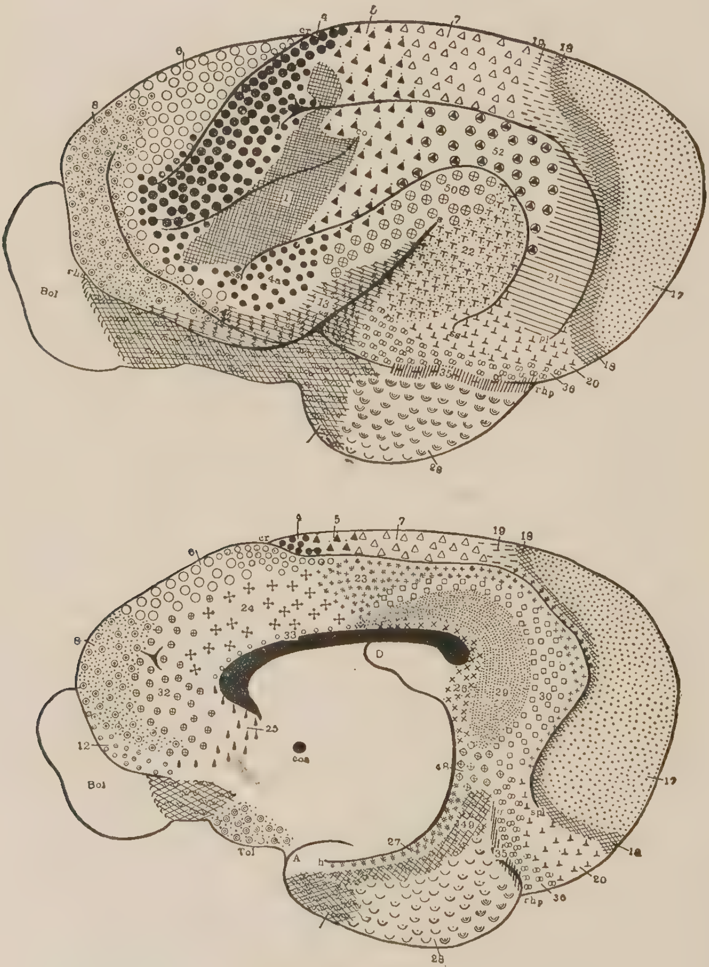
The connections of insular area are in doubt although the anterior part appears to be derived from the piriform cortex. Those of the retrosplenial and cingular regions are not known. A sensory function for the retrosplenial region is suggested by its constancy in the mammals. Edinger has suggested oral sensibility. I have suggested sex and perineal sensibility because the precuneus in the human male is excessively large. The functional significance of the other regions is reasonably clear. Around these main areas and associated with them, bordering zones have been developed which intervene between the main areas. Thus many bordering areas are recognized, some of which acquired individuality early, as for example, the inferior parietal and the middle temporal.





Figs. 195, 196. Cortical areas of a rabbit (Brodmann).

The cortical areas in the smooth brain of the rabbit (fig. 195) show that the cortex of this special rodent is divisible into about twenty different areas consisting of the nine main ones and a larger number of subsidiary ones. The motor (4) and sensory (1–3) regions are in front. Behind them is the parietal region. In the occipital region is the visual area (17). Ventrally is the temporal region. Along the rhinal fissure is the insular region. The frontal tip represents a small frontal region. On the medial side are seen the cingular



Figs. 197, 198. Cortical areas of a kinkajou (Brodmann).

retrosplenial, hippocampal and piriform regions. The bordering zones are particularly evident around the visual temporal and retrosplenial regions.

The **cortical areas of cercoleptes c.** (figs. 197, 198), a small raccoon like animal (also called kinkajou, potto and honey bear), have a typical Carnivore pattern of gyri and sulci imposed upon them.

The cruciate sulcus separates the motor (4) from the frontal region (6). The coronal sulcus separates the motor from the sensory region (1). In the brain of the raccoon (fig. 21) the sensory area appears to be greatly developed and two stellate central sulci replace the coronal. A similar condition is seen in the bear family (fig. 22). The great development of the sensory and motor areas in these animals is probably to be correlated with their arboreal and prehensile habits. Their fissural pattern in this region appears to resemble that of the Primates, though it is a case of convergent evolution. In cercoleptes the temporal area (22) is circumscribed by the suprasylvian sulcus which separates it from the middle temporal (21) and inferior parietal areas (52). The latter is in turn separated from the superior parietal (7) by the lateral sulcus which curves downwards to separate the middle temporal from the visual area. On the medial side the calcarine sulcus separates the visual area from the retrosplenial. The presylvian sulcus is a natural boundary between the lower frontal region and the motor and sensory areas.

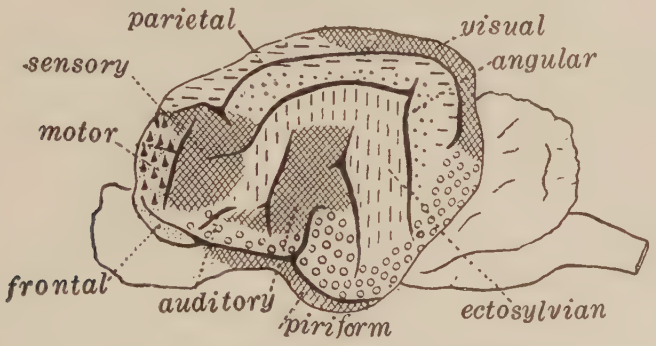


FIG. 199. Cortical areas of a cat (Campbell).

If the **cortical areas of the cat, dog and pig** (figs. 199 to 201) be studied and compared, it will be seen that the cerebral pattern of sulci and gyri expresses in a very remarkable way the natural structural subdivisions of the cerebral cortex. In these figures about eleven regions are recognized in addition to the piriform and hippocampal. The cruciate sulcus separates the medial frontal from the motor regions. The presylvian separates the inferior frontal from the motor and sensory areas which here overgrow it as an operculum. The coronal sulcus separates the motor and sensory regions. The temporal region has two areas, the sylvian (auditory) and ectosylvian which surrounds it. The suprasylvian sulcus separates the ectosylvian area from the sensory, inferior parietal and middle temporal. The lateral sulcus separates the superior parietal from the inferior parietal and extends backward as a lateral boundary of the visual area. In the dog brain (fig. 200) an angular sulcus has appeared separating the angular gyrus from the parieto-occipital area. The lower (fusiform) area of the temporal region is separated from the piriform area by the rhinal fissure and from the visual area by the collateral sulcus. The visual area which in the rabbit and cercoleptes (figs. 195 to 198) is seen to lie chiefly on the lateral surface of the occipital region has been shifted over the tip of the occipital pole

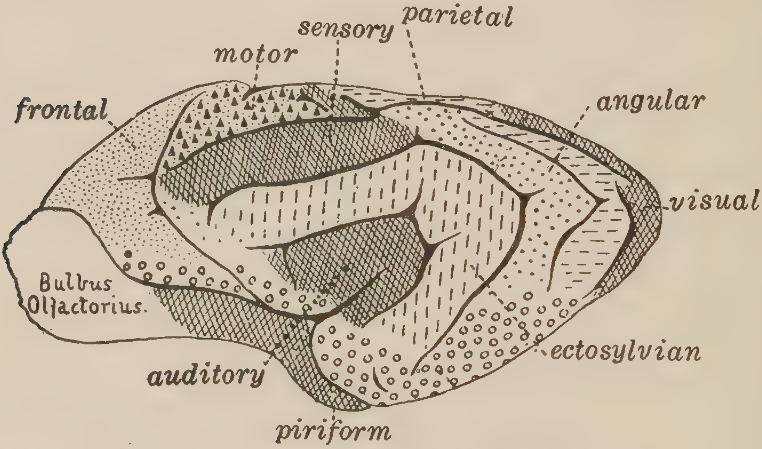


FIG. 200. Cortical areas of a dog (Campbell).

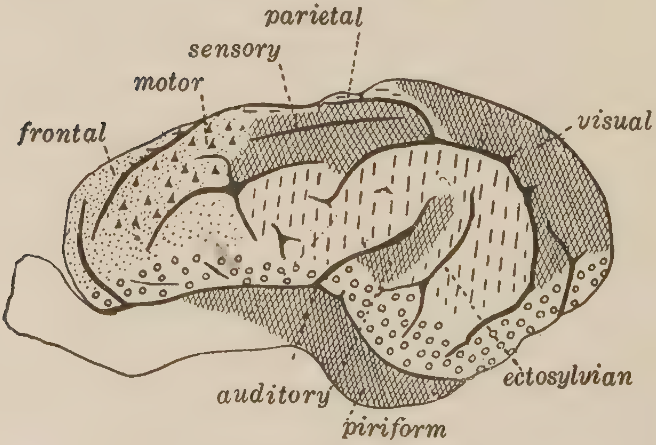


FIG. 201. Cortical areas of a pig (Campbell).

by the backward expansion of the other areas. The calcarine sulcus and the parieto-occipital (intercalary) separate the visual area from the retrosplenial area and cingular region. It is seen that the superior parietal region is not separated from the visual area by a definite sulcus. But in some dogs and other Carnivora, a definite inflexion occurs in the medial border between the parietal and sensory areas. In the pig the intercalary incises the medial border and separates the visual from the parietal area.

The location of the motor area in the Ungulata (fig. 201) is in doubt. Campbell has localized it in the pig lateral to the cruciate sulcus. It is probable that the motor area for the head and snout occurs in this region. Simpson and King have localized it in the sheep medial to the cruciate sulcus.

The **evolution of the eleven cortical regions of the Primates** and their relation to the fissural pattern can be visualized by following each region out in figures 202 to 209. In general the distribution of these main regions is the same as in the lower orders. But on account of the great size of the frontal, temporal and occipital regions the gyral pattern is much altered and many new subsidiary areas are added. The numbers refer to Brodmann's figures.

1. **Precentral region.** The **motor area** (4) in the lower forms is located behind the presylvian and cruciate sulci; in the Primates it is behind the inferior and superior precentral sulci and is enlarged in its dorsal and ventral extent. It is separated from the sensory area by the central sulcus. These sulci are absent in the marmoset, are foreshadowed in the lemurs, but form a constant feature in apes and man. It is a distinguishing feature of the Primate brain that both the superior and inferior frontal regions are enlarged inclosing the older middle frontal region (6) between them. If this view is accepted the analogues of the presylvian and cruciate sulci of the lower forms ought to appear in the position of the inferior precentral and superior precentral sulci. In the frontal lobe of the bear (fig. 22) the cruciate sulcus takes a position resembling that of the superior precentral sulcus of Primates. Beyond this, homologies in the frontal region are futile because in other respects the Primate brain shows a divergent pattern from the outset of its evolution. It is true that in some of the lemurs (fig. 24) a carnivore-like pattern appears but other distinctly Primate features are also present.

A **premotor area** (6) is recognized (by Campbell and Brodmann) which resembles in cell structure the motor area. This is the area that is regarded as sending down the fronto-pontal fibers which discharge into the cerebellum. From their figures it appears that the precentral sulci indicate more or less closely the boundaries of this important accessory motor area. Its extension forward in the inferior frontal gyrus is shown in the figures of Campbell and Smith.

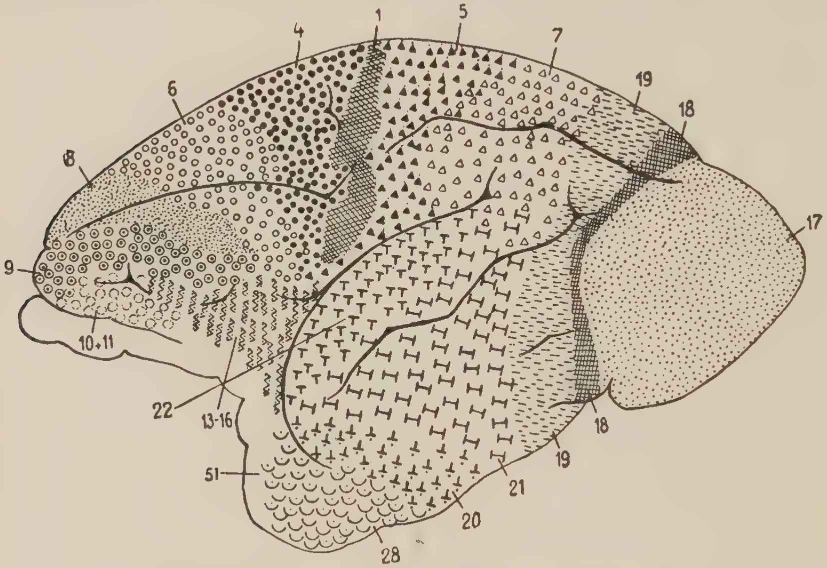


FIG. 202. Cortical areas of the lemur (Brodmann).

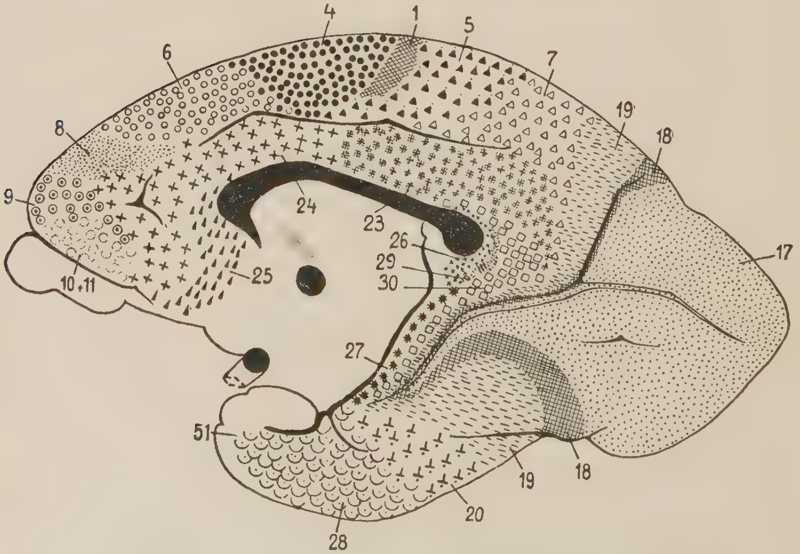
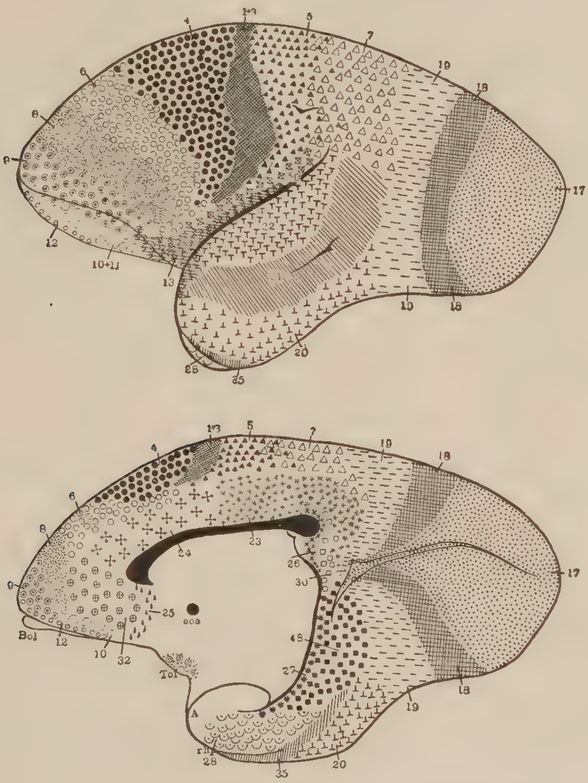


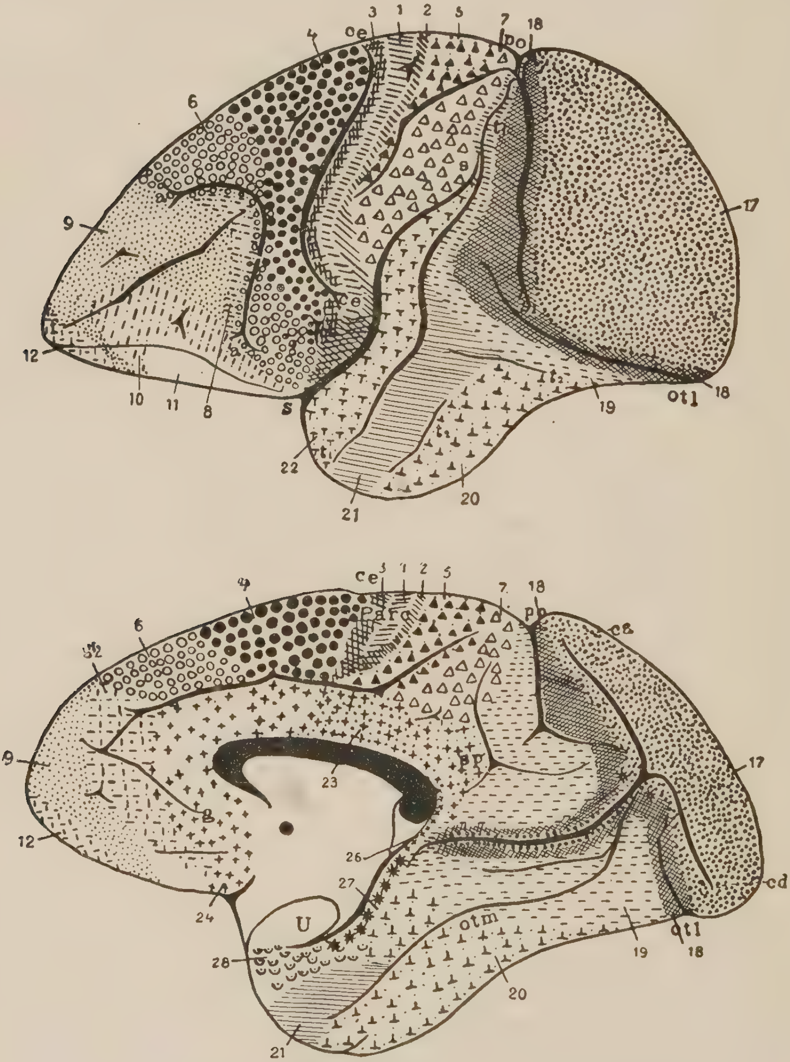
FIG. 203. Cortical areas of the lemur (Brodmann).

2. The **frontal area** (8 and 9) comprises the cortex of the superior, middle and inferior frontal gyri. It may be regarded as an important association area divisible into three parts, each of which stands in relation to the premotor area with which it is in continuity. Thus the lower limbs, upper limbs and head and neck appear to have a prominent and somewhat separated representation in the frontal area. In the apes this area is relatively small in the lower frontal gyrus, but in the human brain it is greatly enlarged (46), a feature of special interest in correlation with the functions of speech. In well-developed human brains it is limited in front by the sulcus radiatus (*rad*) and posteriorly by the frontal transverse branch (*ft*) of the inferior frontal sulcus.



FIGS. 204, 205. Cortical areas of the marmoset (Brodmann).

The **prefrontal area** (10 and 11) is poorly developed in the apes but in man it is one of the most significant areas of the brain to which are attributed the higher psychic functions. It is seen that it does not share the tripartate subdivision of the frontal area in any important way. The fronto-marginal sulcus appears to have an independent origin. The orbital area may be included with the prefrontal.



Figs. 206, 207. Cortical areas of the cercopithecus (Brodmann).

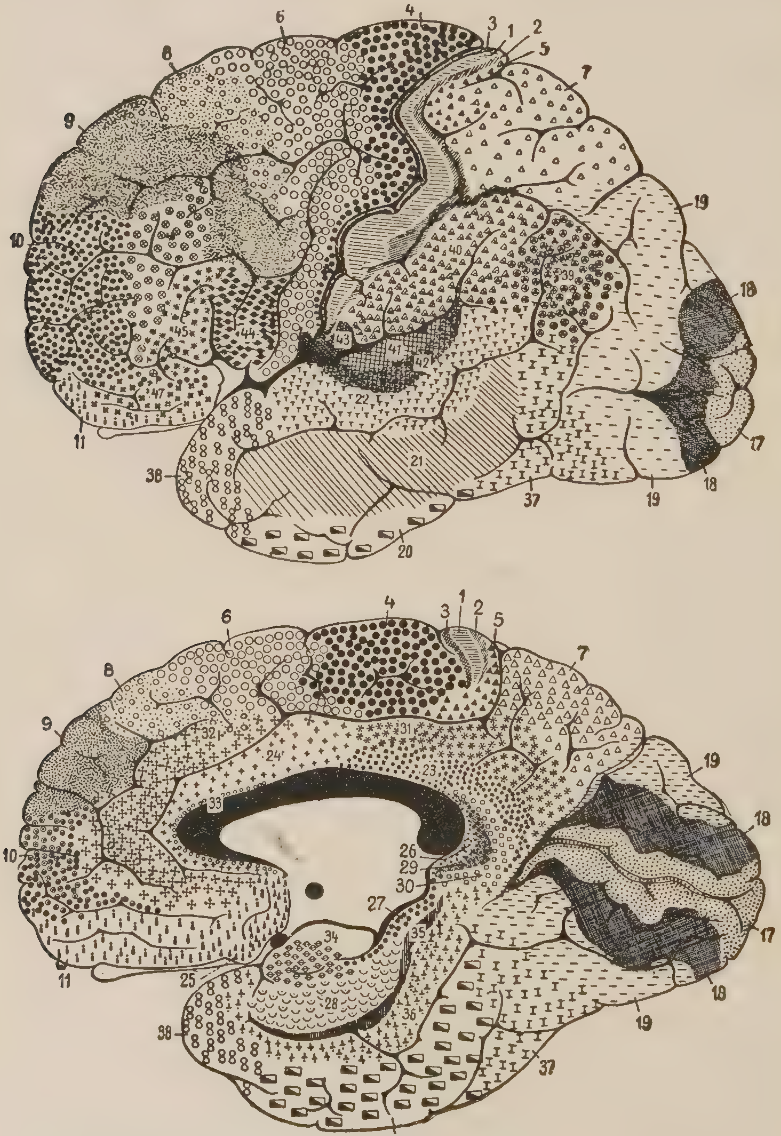
3. **Postcentral** or **sensory area** (1 to 3) includes the cortex of the postcentral gyrus. The central sulcus is a natural boundary between it and the motor area. The postcentral sulci are its posterior boundary although this delimitation is not so precise.

4. **Parietal region.** The **anterior parietal area** (5) appears just behind the postcentral sulci and merges with a **posterior parietal area** (7). Both extend on to the medial surface into the cortex of the precuneus. The intraparietal sulcus is an important line of separation between the **superior** (7) and **inferior** parietal (40) areas. It is regarded as a homologue of the lateral and not of the suprasylvian of the lower forms, though this view is still open to question. It is interesting to note that the postcentral area is continued backward into the parietal region at three levels reminding one of the continuity of the motor area with the superior, middle and inferior frontal gyri.

5. **Temporal region.** The **auditory area** (41) occupies the transverse temporal gyri. Two surrounding bands of cortex (42 and 22) are recognized. The superior temporal sulcus becomes a natural boundary for these. Beyond this is the **middle temporal area** (21), the evolution of which can be traced from rabbit to man. Over the tip of the temporal pole is the temporal polar area (38). Posteriorly is the posterior temporal area (37). On the ventral side are the inferior temporal area (20) and the fusiform area (36), probably related to some function other than the auditory.

6. **Occipital region.** The **visual area** (17) of the Primates is greatly enlarged. As in the Carnivora it has also shifted to the medial side of the occipital pole. It becomes folded, giving rise to the posterior calcarine sulcus. The anterior calcarine and parieto-occipital sulci remain as its anterior boundaries. On the lateral surface the simian cleft (Affenspalte) and the inferior occipital sulci appear as natural boundaries. Along these bounding sulci two bands of modified cortex appear which have been called the para- and peristriate areas. They are poorly developed in the apes, forming the submerged cortex of the parieto-occipital fossa and simian cleft (Affenspalte). In the human brain they are greatly developed, forming on the medial surface the cuneus, parieto-occipital fossa, lingual gyri; on the lateral surface they emerge from the simian sulcus to form the superior and preoccipital areas; likewise they emerge from the inferior occipital sulcus to form the inferior preoccipital gyri. From these causes new sulci and gyri appear in these regions of the human brain, the forerunners of which occur in the depths of the simian sulcus. Such a disruption of the primitive simian sulci also occurs in other regions as in the prefrontal area. It is to be noted that the angular area (39) arises from the most

anterior part of this peristriate area always in close association with the middle temporal area (21). In the apes it is just in front of the



Figs. 208, 209. Cortical areas of the human brain (Brodmann).

simian cleft. The anterior occipital sulcus separates the angular gyrus from its posterior part, the occipito-parietal lobule, which has risen with the preoccipital areas from the interior of the simian cleft. The collateral and transverse collateral sulci become natural boundaries of the visual areas on the medial side.

7. **Cingular region.** The **posterior cingular area** (23) is considerably enlarged and is surrounded by another area (31). They extend forward into the anterior cingular area (24). It is surrounded by the para-cingular area (32).

8. The **insular area** is divisible into a posterior insular area related to the transverse temporal gyri and an anterior insular area related to the piriform area.

9. The **piriform area** covers the region of the uncus and is separated from the fusiform area by the rhinal sulcus. It extends into the anterior insular area.

10. The **hippocampal area** includes the hippocampus, dentate gyrus, subiculum and hippocampal gyrus. The latter extend dorsally into the retrosplenial area which appears to be a related cortex.

11. The **retrosplenial area** (29) surrounded by an accessory area (30) is found behind the splenium of the corpus callosum. It is large in the macrosmatic mammals but in the primates it is considerably reduced.

From the foregoing sketch it will be seen that the fissural pattern is the expression of growth of the various regions and their further subdivision into subsidiary areas.

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CHAPTER 33

FUNCTIONS OF THE CEREBRAL CORTEX

THE old idea of the existence of five senses was doubtless derived from the fact that vision, hearing, feeling, smell and taste have a high degree of representation in consciousness. A large part of the cortex is in fact devoted to the analysis of the four sensory functions

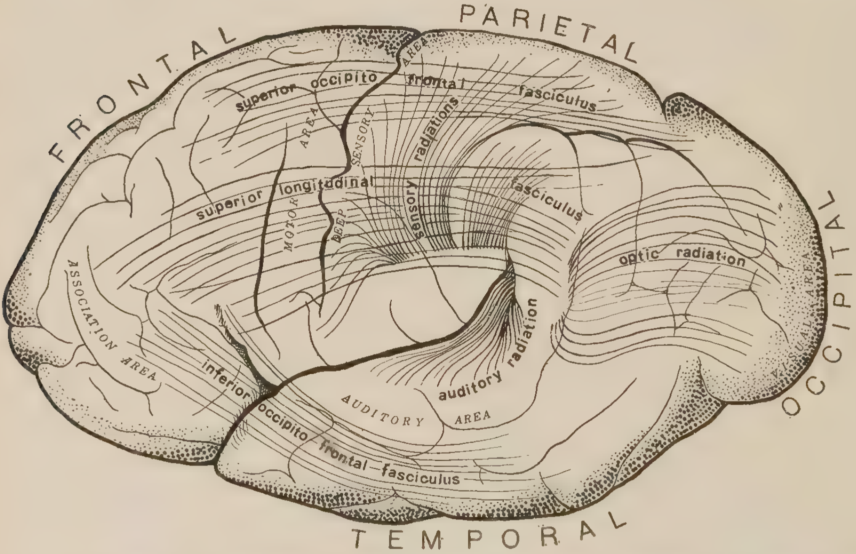

FIG. 210. Plan of the thalamo-cortical radiations and long association bundles in the human brain, $\times \frac{2}{3}$.

of sight, hearing, touch and deep bodily sensibility. Smell and probably also taste are functions of the olfactory brain. The cortex situated behind the motor area of all lower mammals can be looked upon as a generalized sensorium reached by four streams of sensory fibers coming from the thalamus (fig. 210). The optic radiations discharge retinal impulses into the visual area. The auditory radiations discharge cochlear impulses into the superior temporal cortex. The ventral thalamic radiations discharge proprioceptive impulses into the postcentral gyrus while similar radiations discharge impulses of cutaneous sensibility into the inferior and superior parietal lobules. There is little doubt that different parts of the sensory organs have a certain degree of topographical representation in their sensory areas of the cerebral cortex. This is a natural consequence of the chaining of neurones in the afferent paths to the cerebrum, for each chain of fibers in a conduction system can have only a limited region of termination in the cortex, however scattered this may be. Thus for each of the four conduction systems there are many topographical foci in its respective sensory field.

In the Primates and to a much smaller degree in lower animals the primary sensory areas have become surrounded by bordering zones of differential cortex which stand in immediate functional relations to the sensory area. These have been called psycho-sensory areas (figs. 202 to 209) because lesions in them produce psychic sensory disturbances but not necessarily sensory loss. Another important point is that the sensory areas are in intimate connections with these surrounding areas by means of short association fibers and by direct cortical continuity. As will be evident these psycho-sensory areas exhibit some evidences of special function apparently associated with topographical representation in the sensory areas with which they are in immediate relation.

Flechsig has shown that the myelin sheaths of the fibers of the cerebral hemisphere acquire their maturity at various stages in the development of the brain. The thalamo-cortical radiations and projection fibers are myelinated before birth and those of the surrounding areas at later periods. Fiber systems of like functions myelinate at the same time. By the sequence of myelination it has been possible to map out different cortical areas, whose functional significance probably differs considerably.

During the last century a rather rough localization of cerebral functions has been achieved by clinical experience, by physiology, anatomy and psychology. The facts in general are quite concordant. Existence of the localization of the primary sensory and motor functions is sufficiently proved by the evidence of structure alone since definite reception fields such as the retinae, cochleae, deep and cutaneous receptors have been shown to stand in connection with definite cortical areas. As far as known the plan of connections and localizations is consistent throughout the mammalian kingdom. The difficulties have arisen in the attempts to assign specific functions to the areas that surround the sensory and motor areas and in the interpretation of the so-called associative functions. Even in experimental animals some degree of localizations of the psychosensory functions and of the cortical associations has been manifest. This probably grows out of the fact that the topographical distribution which the sensory and motor areas have in the cortex tends to impress upon the contiguous areas a certain consonance of function. That is, these localizations of function develop out of anatomical connections under the influence of discipline and natural selection.

It is now known that the cerebrum is a dual organ; that the right hemisphere coöperates with the left and that one hemisphere may compensate for a considerable loss of substance of the other half. That is, psychic activity, though it normally involves both hemispheres, is not essentially bilateral. This vicarious functioning applies to all areas of the brain and requires an intact corpus callosum. Lesions of the left side affect the mental processes more severely than those of the right side, which may be completely silent. Bilateral lesions, especially those symmetrically located, produce outstanding defects. There is abundant evidence of this kind, that the mechanisms of thought processes have an anteroposterior arrangement in each hemisphere, particularly the left.

From his studies of conditioned reflexes in dogs, Pavlov concludes that: "It becomes obvious that through the medium of the cerebral cortex a great number of environmental changes establish now positive, now negative conditioned reflexes and determine in this manner the different effector activities of the animal organism and its everyday behaviour. All these conditioned reflexes must have definite representation in the cerebral cortex in one or another definite group of cells. One such group of cells must be connected with one definite activity of the organism, another with another activity. One group may determine a positive activity while another may inhibit an activity. The cerebral cortex can accordingly be represented as an exceedingly rich mosaic of functions or as an extremely complicated 'switchboard.' However, in spite of its extreme complexity as a switchboard there are always large spaces reserved for the development of new connections. Moreover, points which are already involved in a definite conditioned activity frequently change their physiologic rôle and become connected with some other activity of the animal." (Conditioned reflexes, page 211.) This view of cerebral localizations is consistent with anatomical, physiological and clinical data. It is to be expected that in so highly differentiated and disciplined cortex as the human, considerably more of such cerebral localization should exist.

It follows from the work of Munk, Pavlov and others that a destructive lesion of any part of the sensory or surrounding areas can not produce a complete loss of its analytic and associative function since other parts of the peripheral end organ remain in structural and functional continuity with uninjured portions of the cortex, and new cortical paths can be formed. This is at least true of the sensory functions of the limbs on account of the greater separateness of their sensory areas in the cortex, but even here there is much overlap of function.

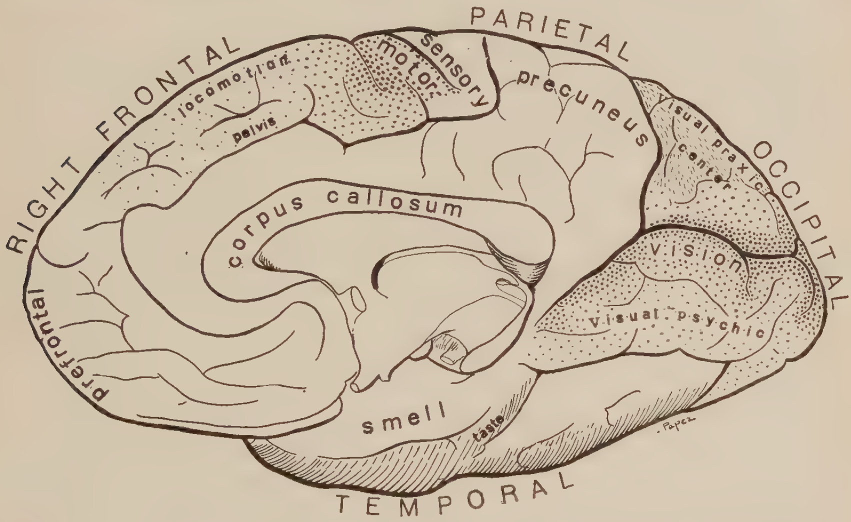

FIG. 211. Medial view of human brain showing functional localization, × $\frac{2}{3}$.

For studies of the analytic, synthetic and associative functions of the visual, auditory and sensory areas, the reader is referred to the last part of this chapter and to Pavlov's monograph on conditioned reflexes.

The visual area (figs. 210 and 212)

In 1855 Panizza found that the optic nerve is connected with the occipital cortex by means of the optic radiations. Later in 1874, Hitzig found that lesions of the posterior part of the dog's brain produced blindness of the opposite eye. Ferrier localized vision in the angular gyrus of the monkey and corresponding regions in dogs, cats and rabbits. Munk showed that bilateral removal of the dorsal part of the occipital region (A) in the dog caused psychical blindness; the dog could see but no longer recognized objects. When the whole of the occipital lobes was removed then the animal became totally blind, a condition known as cortical blindness. The same has been found in monkeys. Beyond the occipital lobes vision also extends to the angular gyrus which lies over the path of the optic radiations. Removal of one occipital lobe causes a bilateral loss of vision most extensive on the opposite side. This is due to the bilateral distribution of the optic tracts to the cerebrum. These symptoms tend to disappear, but when the corpus callosum is cut or the other occipital lobe is removed these symptoms reappear in aggravated form. It has been found that after a few weeks some imperfect form of vision begins to return in any case and that visual conditioned reflexes begin to reappear. This has generally been interpreted that vision is not localized exclusively in the occipital lobes and angular gyrus. But the possibilities of regenerating optic fibers invading surrounding territory has not been excluded. For a more complete discussion of the extirpations see Luciani.

Extensive lesions of the occipital cortex in man cause visual disturbances, psychical blindness and mind blindness. Lesions of the medial surfaces over the calcarine fissure cause the most severe forms of mind blindness. In this way it has been shown that the lingual gyrus and cuneus as far forward as the collateral and parieto-occipital fissures are concerned with vision. On the lateral surface lesions of the superior, middle and ventral occipital gyri also produce hemianopsia. Infant blindness followed by complete optic atrophy leads to reduction of volume of the striate area as well as surrounding occipital cortex.

In psychical blindness some vision and to some extent the perception of form (stereognostic vision) are imperfectly preserved, but the patient may not be able to identify even the most familiar objects. When the lesion is in the upper occipital region there is an inability to copy or guide the hands in any previously well-known manipulations. This leads to the view of Henschen that this is a **visual praxic center** which is connected forward with the middle frontal cortex where the cellular mechanism for guiding the movements of the eyes and hand appears to be located. A direct connection of this area through the internal capsule with tectal centers and cerebellum has been demonstrated.

Word blindness (alexia) is a special form of psychic blindness seen in man when the angular and parieto-occipital gyri are injured. The patient is unable to comprehend the meaning of printed or written words although the powers of speech or handwriting may be retained. The patient is incapable of reading and understanding, although he can see and copy the words correctly. The visual field may not be affected unless the lesion be close to the calcarine gyrus or deep so as to involve the visual radiations. Although such angular lesions are in the so-called association areas there may be no auditory disturbances. Evidence of a similar order on the psychosensory functions of the lingual and inferior occipital region are wanting, but it is suggested that this area stands in topographical relation to the inferior half of the retina which is of much less functional importance than the macula and superior half.

Psychical blindness is a complex disturbance and depends on various factors, such as location, extent and depth of lesion, relations to calcarine area, transcortical connections of the area, the experience, culture and special discipline of the patient. For a more complete discussion see the monographs of Henschen.

The auditory region (fig. 212)

Ferrier (1875) was the first to point out that the center for auditory sensation is in the superior temporal cortex in the ape and in a corresponding area in the dog. By electric stimulation of this region he produced movements of the ear, opening of the eyes, dilation of pupils and movement of the head and eyes in the opposite direction as if the animal were surprised by some unexpected sound. By cautery of the superior temporal gyrus and plugging of the ear on the same side he showed that the animal failed to react to sound. Bilateral destruction caused deafness. Later experiments of Luciani have shown that the auditory function spreads more or less beyond the superior temporal region. It is recognized that the auditory paths are chiefly crossed, that lesions of the surrounding areas cause psychical deafness, that lesions of the superior temporal gyrus cause cortical deafness, that unilateral lesions soon become compensated and that bilateral lesions result in more serious and permanent defects of hearing. According to v. Monakow the cortex of the temporal lobe and especially the superior gyrus is in direct connection with the medial geniculate body by means of the auditory radiations (fig. 210). These and their cells atrophy or completely degenerate when these temporal areas are removed. They are markedly deficient in deaf mutes.

In man clinical evidence also supports this view, for bilateral destruction leads to marked mind deafness. The usual disorder is one of psychic deafness. The patient while perfectly aware of sounds and noises is not able to understand them. It involves disorders of speech, hence it is known as auditory aphasia. According to Kussmaul, this is really word deafness comparable to word blindness. Disturbances of perception and understanding of the sounds of music, words and sentences and grammatical constructions are chiefly involved. The lower or temporal end of the angular gyrus appears to have auditory functions. Lesions of the left temporal lobe are most severe in right-handed individuals and vice versa.

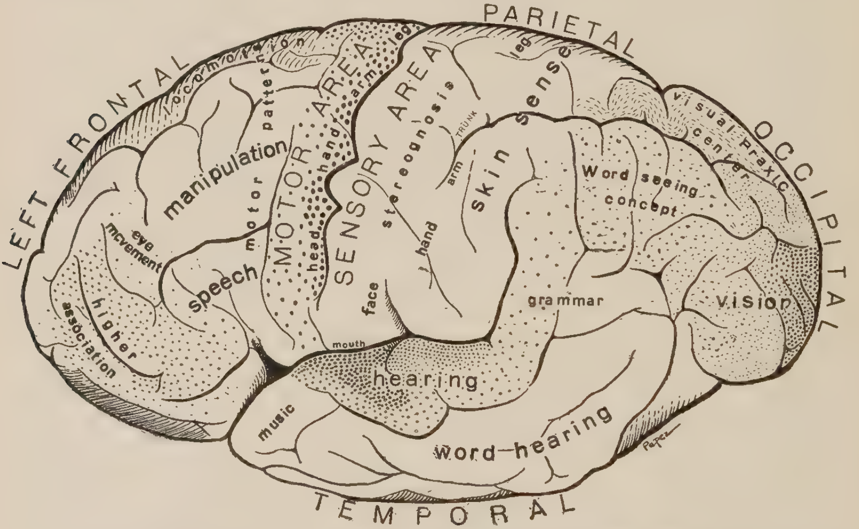

FIG. 212. Lateral view of human brain showing functional localization, × $\frac{2}{3}$.

To what extent the auditory temporal region coöperates with the angular and occipital region in the formation of new associations is uncertain. Some contiguity and overlap of structure seems to be present. That they tend to inhibit each other's activity seems more likely. Both Munk and Pavlov have concluded that their experiments do not support the theory that important functional associations take place between the sensory areas in the so-called association or silent areas of the brain. All that has been so far demonstrated is that each region through its surrounding areas can form various combinations of conditioned reflexes so long as the frontal lobe is intact. The angular gyrus may be an area of mixed sensibilities.

That the temporal region as well as the angular region projects upon the inferior frontal gyrus through the superior longitudinal bundle (figs. 48, 210) seems to offer an explanation of visual as well as auditory aphasia arising from deep lesions as well as from frontal lesions. It would also explain why speech disturbances result from lesions that occupy such a large zone as Marie's quadrangle.

The sensory region (figs. 211 and 212)

The experiments of Munk on dogs indicated that the coronal gyrus is the center for the sensory representation of the upper limb. This depends largely on deep or proprioceptive sensations combined with cutaneous sensibility. When this area is surgically removed it causes a loss of appreciation of contact and pressure on the skin of the fore limb, and also the loss of appreciation of its position, that is, a loss of the motor as well as tactile representation of the fore limb. Munk defined these disturbances as psychical paralysis of sensibility of motion. A similar sensory area for the hind limb is found at a higher level of the postsigmoid gyrus but it is much smaller in extent.

These areas receive the sensory radiations from the thalamus (fig. 210). These areas are not only adjacent to the motor area but closely combined with it in function. Injury of one affects the functions of the other. So it is more convenient to speak of the whole region as sensory-motor. The experiments of Goltz, Mott and others show that the sensory and motor areas are in the main functionally separate, especially in the Primates. A great enlargement of these areas takes place in the raccoons (fig. 21) and bears, animals in whom the functions of standing, climbing and prehension are well developed.

This is the area that projects the large parieto-pontal tract through the internal capsule to the pons. Excitations from this tract reach the cerebellar cortex. The tract appears to arise in large part from the inferior parietal lobule and also from the temporal region. The experiments of Brown tend to show that through this parieto-cerebellar connection facilitation of movement takes place. This is probably one reason for the electrical excitability which this region exhibits.

Below the coronal gyrus is another area for muzzle and facial sensibility. This is larger in dogs than in cats. In the Ungulates (such as the sheep and pig, figure 201) in whom the muzzle sense is much used for securing food this area is very large so that the coronal and motor areas are displaced upwards.

The functional deficiencies that follow operative removal of these areas in animals must be studied soon afterwards; for it is now thought that the opposite hemisphere or regeneration of the afferent fibers compensate for the loss, so that the deficiency symptoms disappear completely in a few weeks, when, too, the subcortical motor mechanisms have become adjusted to the cortical deficiency.

The sensory region may be divided into several foci of function; for the lower limb, for the fore limb, for the head, face and tongue and probably one for the eyes. These are more completely differentiated in the Primates although there is still much overlap.

Clinical observations in man have confirmed the physiological work on monkeys. Luciani, in 1886, and since then many others have concluded that disturbances of cutaneous and muscular sensibilities may result from postcentral lesions without paralysis of movement. No one now denies that sensation can be affected by a lesion of this region of the cerebral cortex. There is also no doubt that the various regions of the body are topographically represented in the postcentral convolution. This means that the various tracts of deep sensibility which bring in sensations from the various regions of the body have each a definite locus of termination in the postcentral gyrus. Lesions of the postcentral gyrus always produce a severe sensory disturbance and the residual loss is permanent.

According to Head, lesions of the upper end of the postcentral gyrus involve sensibilities of the lower limb and lesions of the lower end involve the sensibilities of the face and tongue. Lesions of the middle of the gyrus involve the sensibilities of the upper limb but the functions of face and lower limbs may be involved. For instance when the lesion is in the middle of the postcentral gyrus and the sensory loss affects the thumb and index finger, then the face and tongue tend also to be affected. When the loss is greatest in the little and ring fingers it is the foot that shows some sensory or motor change. It is evident that the fingers are represented topographically in the middle of the gyrus. The thumb below, next to the face area, and the fingers in their order upwards, so that the area of the little finger is nearest that of the foot. Each digit, at least so for a perception of movement is concerned, is a unit. The thenar eminence goes with the thumb; the lateral half of the palm with the index and middle fingers; the medial half with the ring and little fingers and with the wrist. When sensation of the medial side or of the whole hand is involved the wrist, elbow and shoulder and even the foot may show some changes. This is liable to occur when the deeper parts of the gyrus have been injured. The deeper the injury the more certain it is to produce a motor disturbance of the same parts.

The sensibilities of the trunk appear to be deep in the postcentral gyrus.

The farther posteriorly the lesion extends on to the parietal region the more complex the functional disturbance.

It is the functional units of the body rather than any anatomical areas or tissues that are topographically represented in the sensory cortex. Thus the hands and fingers are represented by a very considerable area. Each finger is represented as a more or less stalked sense organ. In this the sensibilities from the skin, joints, bones and muscles are combined into a unitary representation. In the postcentral and parietal region, Head recognized three categories of function more or less combined for each functional region of the body. They are deep sensibility, cutaneous sensibility and stereognosis (or a combination of the two).

Deep sensibility or the function of recognition of the position of the body or limbs in space is indeed one of the most important functions of the cortex. It is localized in the postcentral gyrus. This, on account of its close connections with the motor area and the cerebellum, is also an organ for guiding and controlling movements. This gyrus receives at its various levels afferent fibers from the various functional regions of the body, such as the foot and leg, sole, fingers, hand, face, tongue, etc.

Cutaneous sensibility or recognition and analysis of graded stimuli of touch, pressure, heat and cold that impinge on the skin is the other important function. This is not as homogeneous as deep sensibility. Its physiological varieties probably are dependent on differences in the afferent conduction pattern of the different sensations such as touch, heat, cold, etc. These functions appear to be localized, for the mouth in the foot of the central convolutions, for the face in the same region, for the hand in the inferior parietal lobule and for the leg in the superior parietal lobule. Lesions of these regions produce disturbances of cutaneous sensibility independent of deep sensibility.

Stereognosis and the appreciation of similarity and differences of objects brought in contact with the surface of the body is another faculty of the sensory cortex. This faculty is most altered when the lesion tends to involve the postcentral gyrus and lies in the zone (of mixed sensibilities) between this gyrus and the parietal lobules. It is probably a derivative of the deep and cutaneous sensibilities.

The location of these three functions in the postcentral and parietal lobules can be determined from the site of the lesions. An upper leg area, a middle hand area and a lower face area are recognized. When the centers for either leg or face are involved as by high and by low lesions, one form or another of hand sensibility may be entirely unaffected or show slight alterations. But when the lesion lies directly over the middle of the postcentral gyrus the spacial appreciation is profoundly diminished in the hand, and also the power of recognizing the form and weight of objects (stereognosis). In such cases tactile sensibility is often not disturbed even to fine tests and the sensations in the leg and face may be quite unaffected. When the lesion involves the supramarginal gyrus tactile sensibility of the hand is profoundly affected. When the lesion is over the superior parietal gyrus the tactile sensibility of the leg is affected. A lesion at the lower end of the postcentral convolution involves facial sensibility. Thus it is possible to construct a zone from the lower end of the central convolutions, over the supramarginal gyrus to the superior parietal lobule which deals with cutaneous sensibility. A lesion in this area must be extensive or severe before it involves a loss of thermal sensibility.

There is little doubt that the representation of the sensory functions of the face are in the cortex at the lower end of the central gyri. Therefore the trigeminal centers of the thalamus must project their fibers on this area. Oral and tongue sensibility appear to be in this region also and possibly are on the opercular surface. There is a possible relation between this area and the claustrum. Pavlov has shown that conditioned reflexes from oral sensations can be formed when all other reflexes are lost after extirpation of the frontal lobes.

The motor area (figs. 211 and 212)

In 1861 Broca showed that lesions of the inferior frontal convolution produced a disturbance (aphemia) or loss of speech (dysarthria). He showed that this gyrus is the cerebral organ where the motor patterns for the articulation of speech are located. Much evidence of the same order has since amplified and sustained the doctrine of cerebral localization in its general outlines. Various disturbances of thought processes, of learning, speech, mobility and general intelligence are produced by lesions of the human cortex in various locations. It is only necessary that the lesion be large or irritative in nature and located in a functional area or so as to interrupt its transcortical connections. It has long been known that lesions in the motor region or at the genu of the internal capsule cause voluntary motor paralysis.

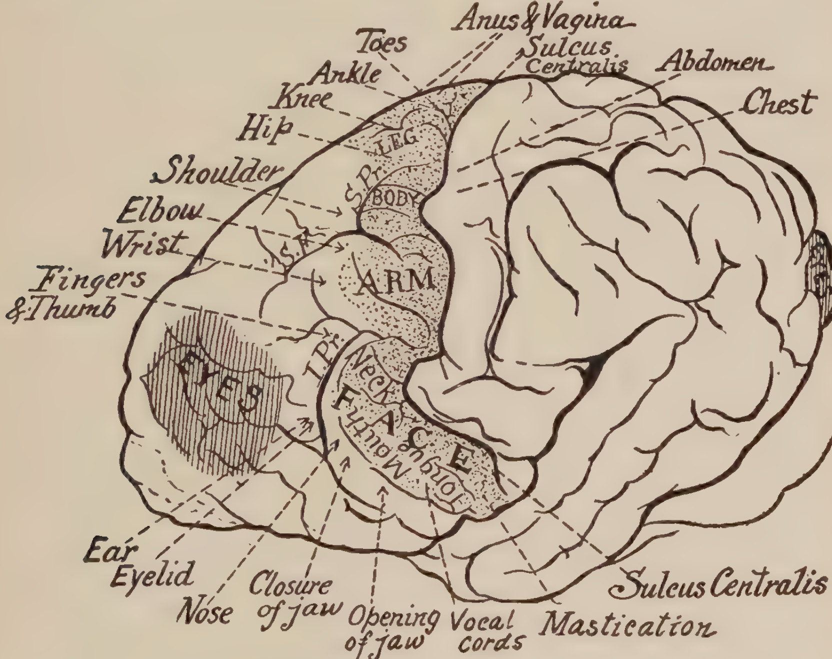

FIG. 213. Excitable motor centers in the brain of a chimpanzee. Grunbaum and Sherrington.

In 1870 Fritsch, while operating on a wounded soldier, applied the galvanic current to the precentral region and observed twitchings of muscles on the other side of the body. This led to his experiments on dogs. Fritsch and Hitzig showed that the region of the sigmoid gyrus is electrically excitable, producing movements of groups of muscles on the other side of the body. The excitable area for the lower limb was localized in the dorsal part of the posterior sigmoid gyrus, for the upper limb in the lateral part, and for the head and neck in the anterior sigmoid gyrus. The experiments of Ferrier extended these observations and showed that the motor reactions evoked by faradization of the cortex had a marked purposive character analagous to those which the animal voluntarily performs under normal conditions of life.

In addition to the localization in the motor area Ferrier showed that excitable points exist in the coronal, suprasylvian and ectosylvian gyri. These experiments throw some light on the localization of excitable points in regions that are now known to be sensory. Stimulation of the angular and suprasylvian gyri excites movements of the eyes; of the ectosylvian, movements of the face; of the cortex back of the lower end of the presylvian sulcus, movements of the tongue and mouth. In the ape, cercopithecus, Ferrier also localized the excitable points in the senso-motor region.

In the higher apes a similar localization has been ascertained by Beevor and Horsley, Grunbaum and Sherrington and others. It appears that in addition to the motor area, the premotor area is also excitable (fig. 213), and that there is a special motor center for the eyes and head in the lower area of the middle frontal gyrus.

In man, Ferrier, Bechterew and Krause have localized the excitable points in the precentral gyrus, figures of which will be found in text books on the subject.

Bubnoff and Heidenhain showed that the motor cortex inhibits reflex motor contractions; and it is now admitted that the motor centers are capable of both excitor and inhibitory reactions. The experiments of Sherrington show that the excitability of points in the precentral area is facilitated by stimulation of similarly located points in the postcentral gyrus; but stronger currents are necessary to evoke motor responses from the postcentral region. Applied to the frontal region strong stimuli tend to inhibit the motor area. Stimulation of occipital, parietal and temporal regions is without any certain effect. It is admitted that of all the sensory regions of the cortex the postcentral region is the one most closely associated in function with the motor area and most susceptible to motor excitation.

Sherrington showed that some motor points produce contraction of a group of muscles and at the same time relaxation or depression of tonus of the antagonist muscles. He was able to demonstrate this reciprocal innervation in the muscles of the eyeball (of the cat) as well as flexors and extensors of the limbs. These reactions from the stimulation of the cortex probably follow the reciprocal innervation of the lower arcs upon which they play.

The premotor area (figs. 208–209)

The premotor area is structurally and functionally related to the motor area. A comparison of these areas in Chapter 32 will show that they arise and develop together as two fundamental areas of the frontal lobes. It is chiefly upon this premotor area that the parietal, occipital and temporal regions of the brain project their association fasciculi (Bianchi, Chapter VII). These fasciculi provide the important transcortical mechanisms for shifting the focus of psychic activity from the sensory to the motor sphere. This possibly accounts for the subconscious intervals which occur between certain phases of psychic processes, and for sensory disturbances following precentral lesions. The important transcortical connections for these functions appear to be the antroposterior ones, but through the fibers of the corpus callosum the functions of one side are merged with those of the other side and may thus compensate each other in case of partial unilateral loss.

The premotor area in addition to its direct connection with the motor area projects a large tract of fibers into the pons which discharges its excitations into the cerebellar cortex. According to Monakow the red nucleus also is connected with the frontal cortex. Stimulation of this area also produces motor responses, though not uniformly so. Inhibitory responses have been more consistently demonstrated. Lesions of this area tend to disturb markedly the motor reactions though they do not abolish the motor function. Thus a lesion of the posterior part of the inferior frontal gyrus produces a marked disturbance of articulation (dysarthria) but not a complete paralysis of vocalization (anarthria). A lesion of the posterior end of the middle frontal convolutions where it joins the motor area produces a marked disturbance of manipulation (apraxia) but not a loss of the motor functions. A lesion in the posterior part of the upper frontal convolution produces a similar disturbance of lower limb movements. Lesions of the genu of the corpus callosum through which the two frontal lobes are joined by fibers also cause apraxia. This shows that the motor and premotor areas of the two sides have an important synergic function. Pressure on the premotor area causes a condition of perseveration of muscular movements in which the attitude or movements cannot be easily altered, initiated or stopped (resembling Thomsen's disease). The premotor area may be considered as the primary region for the formation and memory of motor patterns.

Lesions between the lower and middle frontal sulci cause disturbances of eye movements. This is the region in which Sherrington demonstrated oculomotor innervation in the orang.

The prefrontal and orbital regions (figs. 208–209)

This area is highly developed in man. It stands in most immediate relation to the premotor area but the subdivisions into the upper, middle and lower parts are by no means as clear. Its chief connection appears to be with the occipital and temporal regions by the longitudinal association bundles. The fibers of these probably pass in both directions. These areas are most highly developed in literary and scholastic people, especially the orbitomarginal area around the sulcus radiatus. Lesions of these areas interfere with the transcortical functions such as internal speech, thinking and reasoning and the ability to grasp or understand a situation as a whole (Gestalt). These higher psychic functions are quite independent of the motor reactions. The memory of motor reactions is also impaired in such lesions so that forgetfulness, absentmindedness and loss of initiative and lack of responsibility are also symptoms. When these higher psychic functions are in abeyance an irresponsible dream state follows in which the sensory experiences predominate.

Through the corpus callosum the two frontal regions are brought into synergic activity and in a young individual the area of one side may compensate to a considerable extent for injury of the other. The higher psychic functions are most highly developed on the left side.

Experiments of Bianchi on the frontal lobes of apes in a general way favor these interpretations of frontal lobe functions in man.

Goltz found that when both frontal lobes of dogs had been mutilated they lost the power of voluntarily controlling the lower reflex arcs. The dogs also became impulsive and aggressive, ill-tempered, restless and difficult to manage.

According to Pavlov complete extirpation of both frontal lobes of dogs destroys all motor reactions that depend on previously formed associations in the cortex. There is a complete and permanent loss of ability to form new ones so long as the animal lives, which is seldom as long as three years. There is one exception to this rule and that is the water reflex. Water or other substances introduced into the mouth will combine to produce new associational responses (conditioned reflexes). This means that oral sensibility has a special outlet which is not mediated through the main part of the frontal lobe. It may be effected through the olfactory brain or striatum. These experiments of Pavlov show that all associational responses excepting those of oral origin are transcortical and must be effected through foci in the frontal lobes. By analogy these deductions may be applied to the higher psychic functions in man which appear to be intimately derived from the processes of speech, manipulation, eye movements, etc. There is no sufficient evidence as Munk first observed that higher associations can take place between the visual, auditory and general sensory areas back of the motor region. This does not deny to the sensory regions of the brain the faculties of sensory analysis, of simple sensory fusions and reactions.

General considerations

The motor areas and the frontal lobes are very small in the lower orders and remain small in the macrosmatic forms. The cortical areas in the smooth brain animals are quite homogeneous and too closely related to have even a small measure of independent function.

In these lower mammals the lower motor systems (Chapter 24), such as the spinal, vestibular, cerebellar, tectal and striatal, are highly organized on a reflex plane for the performance of the different kinds of motor responses which depend upon repetition, reinforcement and chaining of reflexes. The lower motor systems are coördinated to produce a summated effect sufficient for any of the ordinary purposive responses. They may even exhibit a considerable amount of variability depending on the intensity and combination of the different stimuli that enter into the act. They, therefore, may be responsive to certain kinds of learning as exhibited by maze tests of animals whose cortex has been partly mutilated. It seems that the early mammalian cortex is at first most highly developed in the regions of the sensory analyzers. In fact the cortex of the lower mammals can be looked upon as merely a generalized sensorium reached by fibers of diverse sensibilities. These areas may augment or inhibit each other or the activity of the small motor area. A more important part is played by the olfactory cortex. And this remains true to a large extent in brains of the larger macrosmatic animals. In these much depends upon the integrity of the olfactory brain and the striatum which can mediate many of the highly purposive and associative responses.

Very early the sensory cortex acquires direct connections with the underlying reflex systems. The sensory areas project fibers upon the tectum and through the pons upon the cerebellar cortex. The sub-thalamus also appears to receive projection fibers from the sensory regions. The motor nuclei are not directly involved. A large amount of animal reactions, behavior and so-called animal intelligence and intuition is probably mediated by these short circuits through the sensory areas of the cerebrum acting directly on the reflex centers. Experiments have shown that the true voluntary motor functions are slight or insignificant in the small smooth-brained mammals.

It is only in the higher arboreal apes and particularly in man that to this impressionistic kind of mentality there are added the associative functions of the frontal lobes which tend to initiate, guide and refine their movements through the use of the great cerebro-pontal and cerebro-spinal tracts. The higher associative functions which involve intelligence, thought processes and learning most likely depend on the development of the long association bundles and the frontal lobes. The cingulum and subcallosal bundles of the lower mammals become greatly enlarged. In the Primates the superior longitudinal bundle and the occipito-frontal bundles become very important structures. The effect of the frontal cortex is to add to this diversified mechanism its own associative or selective activity derived from the experience of the sensory analyzers. In homo sapiens a great prefrontal area is added and he is capable of recalling previous sensory experiences, of carrying on internal speech and higher psychic activity quite emancipated from the actual use of his motor apparatus.

Zones of aphasia

Figure 214 shows the location of lesions which cause various kinds of aphasia characterized by disturbances of the sensory, motor and thought processes of speech. The relations of the lesions to the gyri should be noted from the figure.

A. The syndrome of zone A consists of a dysarthria involving at the same time intonation, articulation and rapidity of speech. Effort, premonitory hesitation and spasmodicity are marked features of the speech in these cases. Aphasic troubles are slight and include principally difficulty in the facility of reading, sometimes of writing and calculation. Lesions in the posterior part of this zone cause the most persistent syndromes and are associated with facial paresis.

B. The syndrome of zone B is a mixture of aphasia and apraxia. It consists of a global aphasia involving all the elements of speech. The lesion is over the superior longitudinal bundle. There is usually a slight brachial monoplegia, almost always a hemianesthesia and in certain cases a bilateral ideomotor apraxia. There is no hemianopsia because the optic radiations are not affected.

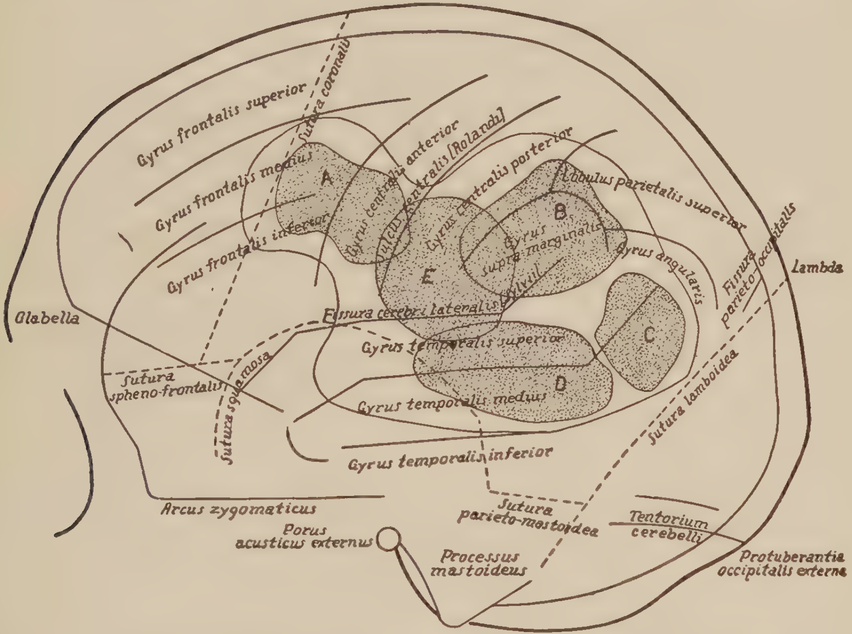

FIG. 214. Zones of aphasia, copied from Marie and Foix by P. Bailey, Archiv. Neur. and Psychiat. 11, 1924.

C. The syndrome of zone C is characterized by the predominance of inability to read (alexia) which is almost absolute. Writing is relatively intact. Comprehension of speech and calculation are involved. Anarthria is absent. There is always a half blindness (hemianopsia); sometimes in the form of a quadrant defect. The lesion is over the optic radiations.

D. The syndrome of zone D is the purest. Anarthria is practically absent. The aphasia affects particularly the denomination of objects (loss of vocabulary). Comprehension of speech, reading, writing and calculation are equally affected. Intelligence is diminished. Hemiplegia is absent. Hemianopsia is present, often in quadrant form. The lesion is over the optic radiations.

E. The syndrome of zone E comprises a marked hemiplegia, serious diminution of general intelligence and a global aphasia in which all elements of speech are involved. Speech is reduced to a few words, and the patient comprehends only the simplest orders. Reading, writing and calculation are practically impossible. There is no hemianopsia and no apraxia. The lesion is over the superior longitudinal bundle.

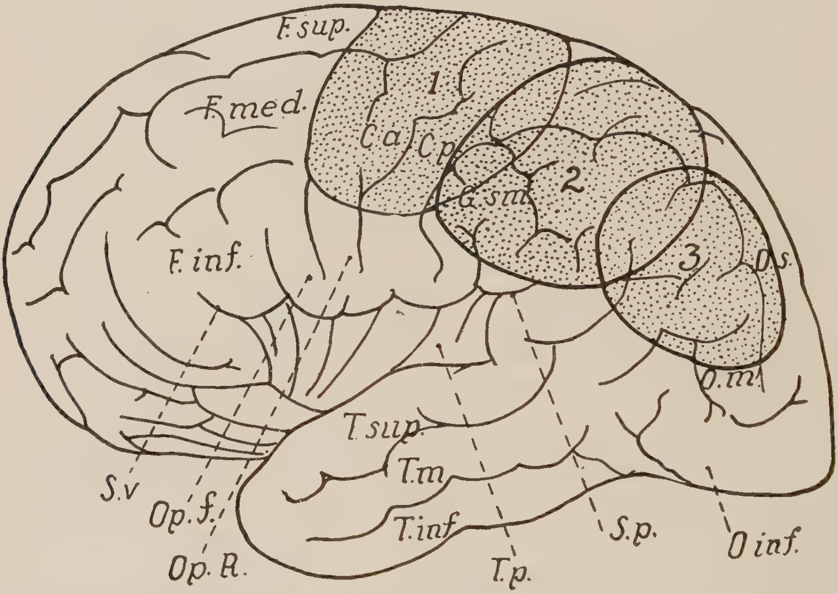

Fig. 215. Zones of apraxia, copied from Liepman by P. Bailey, Archiv. Neur. and Psychiat. 11, 1924.

Zones of apraxia

Figure 215 shows the location of lesions which cause various kinds of apraxia, characterized by disturbances of movement and the sensations and thought processes dealing with movement.

1. **Gliedkinetic apraxia:** Distorted, incomplete, amorphous movements, usually localized. Same as **Motor apraxia** of Foix, inability to perform voluntary purposive movements. Lesion is limited to senso-motor region or corpus callosum.

2. **Ideokinetic apraxia:** Simple movements are well performed except when patient wills to do them. Disturbed initiation of movement and substitution occurs. Sensory changes and paresis of the

opposite side. Same as ideational apraxia of Foix; loss of idea of the motor act which may be performed perfectly in imitation of another. Visual ideomotor function is preserved. Lesion is limited to postcentral and parietal region, especially to the supramarginal gyrus (*B* in fig. 214), causes bilateral apraxia and syndrome of zone B.

3. **Ideational apraxia:** Loss of idea and memory of acts, aphasia. A maladdress which affects the performance of successive movements of the entire body musculature, though some individual acts may be well done. Same as **ideomotor apraxia** of Foix. It is usually bilateral. Lesion is in parieto-occipital, superior occipital and paroccipital regions, the visual praxic center of Henschen (figs. 211, 212).

It is from such information that functional charts of the cerebral cortex such as are shown in figures 211 and 212 have been constructed.

Cortical associations and adaptative responses (conditioned reflexes)

Cortical associations in dogs have been subjected to an extensive study by Pavlov of Petrograd and his associates. They have devised a new method of adapting or conditioning innate reflexes (such as secretion of saliva when food or acid are introduced into the mouth) so that they will respond to a new and entirely different but specific stimulus. These adaptative responses are called in Pavlov's laboratory " conditioned reflexes."

Bechterew also at Petrograd who followed Pavlov used the method of conditioning innate motor responses such as moving the leg when a painful stimulus is applied to the skin.

The great merit of this work of Pavlov and his followers is that it provides a new and accurate physiological method of studying new cortical association which may be used to evoke the response of a reflex arc. They have been able to study (1) the fundamental conditions necessary to the formation of such new associations, (2) the relation of one of these conditioned responses to another, and (3) the relation of the conditioned response to various external and internal stimuli. These studies have thrown direct light on the **analysis of** different **stimuli in the cortex** and the **associations** that may occur between them under definite conditions as well as **cortical inhibition.**

It is known that all sense organs that respond to stimuli, by means of the afferent nerve fiber exert an exciting influence on their appropriate reflex centers and these in turn influence some motor neurons that regulate the functions of some peripheral organs such as a muscle or a gland. This is the fundamental reflex arc.

It is also a fact that the afferent arms of the somatic reflex arcs and of the special sense organs are connected with the cerebral cortex; cutaneous organs by the spino-thalamic and thalamo cortical tracts; cochlea by the lateral lemniscus and thalamo-cortical tracts; vision by optic tracts and the radiations of Gratiolet and smell by the system of olfactory tracts.

The cortex, then, is not a single organ but a combination of several receptive organs each of which receives and is capable of analyzing impulses of widely different character. We know that each of these analyzing organs is located in a different area of the brain, and that between these sensory areas there exist other non-sensory areas known as "association areas" (Flechsig), because they stand in connection with each other and with the sensory areas by means of subcortical fiber tracts.

In contrast to this varied receptive function there is but one special motor area in the cortex. The efferent paths from this cortex are restricted to the pyramidal tracts, the cerebro-pontal-cerebellar tracts and the fornix. But it has been shown by Ferrier, Sherrington and others that the motor area consists of a complex of motor centers. These supply not only lower centers for individual muscles but lower centers for associated muscle groups much as these are arranged for the performance of simple as well as complex allied reflexes. Each of these motor centers is connected by means of some of the pyramidal fibers with the lower reflex arcs of the brain stem or spinal cord. Through the afferent tracts the various arcs are connected with the sensory center in the cortex and this in turn with its appropriate motor center by means of subcortical connections. Thus the sensory centers for lower limbs is in upper postcentral and parietal gyri, the sensory areas for upper limb in the middle postcentral and inferior parietal gyri. The sensory centers for face and tongue are in the lower opercular end of parietal and postcentral gyri.

The respective motor centers for these are directly in front in the precentral region closely associated with the sensory centers. We are compelled to recognize in the cortex a certain inherent arrangement of the sensory as well as motor centers.

Pavlov and his co-workers have shown that the cortex is an organ in which there exists the mechanism for the formation of temporary connections or associations of any of the afferent sensibilities with various motor responses which in turn can modify or adapt the reflex movements to a changing environment.

Unconditioned reflexes are special **inborn reflexes** which every animal and individual exhibits. The nature of these is favorable, purposive and invariable, and depends on reflex arcs which exist throughout the brain stem and cord more or less independent of the cerebral cortex; winking, pupillary and conjugate eye movements, sneezing, coughing, vaso-constriction, respiration, salivation, urination, parturition, swallowing, etc. These reflexes are stereotyped species reactions. Since most of them are not influenced by various conditions of external environment except the adequate stimulus necessary to evoke them they are called inborn or unconditioned reflexes.

Conditioned Reflexes. There are other reflex reactions which though inborn have a connection with the cerebral cortex and can be modified by changing condition in the external environment. For example, almost every movement of the limbs and body can be altered by activity in the cerebral cortex depending on changing environment, appreciated through eyes or other sense organs. This is the system of reflexes used by Bechterew. The salivary reflex, though a very strong inborn reflex since it is used in the feeding habits of the animal, has also very extensive cortical connections, and can be modified by changing environment. This is the system used by Pavlov.

Natural conditioned reflexes are reflexes of this kind that have grown up during the lifetime of the animal in response to the environment through the different sense organs. They are essentially due to the influence of one or another different sensory system over an inborn reflex arc. Example: presence of food in the mouth produces secretion of saliva, an inborn unconditional reflex. Sight of food soon followed by its presence in the mouth produces flow of saliva. If this association of sight of food and its immediate presence is often repeated it will become established as a natural conditioned reflex. Thus most of the common activities of animals and men are natural conditioned reflexes mediated by more or less well established arcs through the cortex.

Artificial conditioned reflexes are these same reflexes subjected to a new and artificially produced environment for purposes of experimentally studying these cortical processes.

Method of producing artificial conditioned reflexes. An inborn reflex is selected that can be easily and invariably evoked by an appropriate stimulus. Examples: Pavlov uses food or acid in the mouth to produce a flow of saliva. Bechterew uses electric stimulus to skin of leg to produce a defense reaction.

Then another mode of stimulation quite unusual or artificial is so arranged that it can be applied at the will of the observer. Example: contact with skin in some other part of the body, visual stimulus like dark or light or circle, etc., or auditory stimulus like the sounding of a tuning fork, bell, etc. Such a stimulus may or may not evoke an external response. In any case it should be as indifferent as possible as far as the conditioned reaction that is studied is concerned.

This second indifferent stimulus is always applied first and is followed immediately by an appropriate stimulus to evoke the response of salivary secretion or leg movement as the case may be. Thus if a visual condition is desired, a letter A, or a light or dark figure is exhibited as the first stimulus and is immediately followed by food which evokes a flow of saliva. If an auditory condition is desired the sound of a bell or tuning fork is first exhibited followed at once by food which evokes the flow of saliva. If an olfactory condition is desired a smelling substance is exhibited first, followed at once by food which elicits the secretion of saliva. If a cutaneous condition is wanted a hot rod, pin, or some other contact is used, followed at once by food which elicits a flow of saliva. When any one of these combinations of individual conditioning and adequate stimuli have been repeated conjointly a number of times, 10 to 50 on successive days, a temporary association (or connection) is formed in the cortex of the animal; so that when the individual conditioning stimulus alone is exhibited the salivary response occurs in spite of the total absence of the adequate stimulus (food). This is the method used by Pavlov.

In the same way motor responses may be elicited by an electric stimulus applied to the skin. Such a stimulus is painful and the invariable response is a defensive flexion or stamping of the foot. Any other stimulus may be used as a conditioning one, such as sight of an object, smell, sound or cutaneous stimulus in some other part of the body. When the stimuli have been repeated quite a number of times a temporary connection is formed in the cortex, so that when the conditioning stimulus alone is applied the defense movement of the limb ensues despite the total absence of the adequate stimulus (painful electric shock). This is the method employed by Bechterew and Beritoff.

The mechanism which is thus revealed in the brain is that of a **temporary connection,** revealed by the fact that any inactive or indifferent stimulus combined several times in succession with an active stimulus which produces a motor reflex may then itself excite this reflex. A special, though temporary, connection in the brain is thus established between external artificial stimulus and the active portion of the organism.

The analysis of the special conditioning stimulus in the sensory areas must be effected, so that a temporary connection is not established to all stimuli of a given kind. This can be shown in the following instance. The association may be formed in response to a single musical note though all other sounds of the same or other musical instruments evoke no response. The analyzing system may be entirely independent of the reflex system with which it makes these temporary associations. The analyzer in one instance may be the retina, optic tracts, geniculate bodies and visual cortex. In another instance it may be the cochlea, lateral lemniscus and cochlear centers and auditory area in the temporal lobe. In still other instances it may be the cutaneous end organ, spino-thalamo-cortical tracts and parietal cortex. Then again it may be the muscle spindle, medial lemniscus, thalamo-cortical fibers and the postcentral gyrus. Any one of these analyzers may enter in the cortex into a temporary association with a definite motor reflex system if it is subjected to simultaneous stimulation with the latter.

1st Law: Generalized Irradiation. During the early period of the formation of such associations in the cortex each new association in the cortex is generalized. For instance, if a definite salivary response is established to a definite sound of a tone variator, the response may be at first evoked not only by this sound but also by other sounds of the same and other instruments, and sometimes by various noises (P. and Mishtoff). Pavlov believes that this is due to a wide or diffuse irradiation from the auditory center, from visual center or cutaneous centers as the case may be. Since there is, at the time, no other irradiation going on the new disturbance irradiates beyond the limits of the auditory area into other areas.

According to Beritoff the irradiation of the excitation spreads over the whole cortex in a fraction of a second and after the stimulus ceases the duration of the excitation in each part depends entirely on its just previous or immediate functional state. This interval may be as long as two minutes. However, such a response to a more generalized stimulus is more apt to be more generalized itself than where the stimulation is simultaneous with a specific one. Pavlov explains this as due to the attraction that the innate arc has for the irradiation of the conditioning stimulus. Or it may be explained as a phenomenon of facilitation or summation between the local and the general processes of irradiation. Any new or unusual event or disturbance may inhibit these newly formed cortical connections. Example: patter of rain on roof, etc. For this reason conditions must be controlled. It must, however, be stated that under normal conditions of life the resulting response depends upon a greater number of competing conditions and sometimes no obvious result happens at all. Thus various temporary associations are formed and we have conditioned reflexes. The condition is one imposed temporarily on the reflex arc by some other analyzer than the one to which it habitually responds. Thus sometimes one and sometimes another element in the environment may be a signal for food for an animal, and temporary associations only can be useful to the organism if he has to find his food in various ways under varying conditions.

2nd Law: Differentiation of the reflex (or specificity of the reflex). When such a conditioning combination is repeated the analysis becomes more and more specific and the generalized irradiation becomes more and more restricted. Thus, first, noises that differ most from the experimental sound and later those similar to it cease to evoke the response. (100 beats per min. = response; 90 or 104 = no response.) This shrinkage of the cortical irradiation and its concentration to smaller and definite parts and paths in the cerebral cortex is explained as due to a resistance or inhibitory state that is developed in the surrounding parts of the cortex.

This second law of the differentiation of the conditioned reflex into a specific limited response depends upon the active development of a peculiar process in the surrounding parts of the brain known as internal inhibition. It is an active process which must be distinguished from tonic inhibition as well as from sleep (absence of both).

Cortical (internal) **inhibition.** It may be assumed that during sleep there is a cessation of cerebral activity, or a zero state of rest or inactivity. It is supposed that this same condition probably occurs in the cerebellar cortex and probably also in other centers when cellular activity ceases or falls below the level of producing any neurogenic manifestations. The active cortex (waking hours) on the other hand exhibits the phenomena of **tonic inhibition** which we have already seen existed in the reflex arcs as well as in all the tracts and centers which play upon the arcs. Pavlov and his co-workers have shown that such inhibitory influences exist between centers in the cerebral cortex. The individual analyzer centers tend to resist the spread of excitation from some one center. It may also be assumed that the spread of excitation from any of the sensory analytic foci to the motor foci is favored by the inherent arrangement of subcortical connection between the analyzers and the motor foci. The conduction paths between the two, largely cellular and synaptic, become more permeable and less resistant to the conditioning impulse so long as they are reinforced by the unconditioned or natural circuit. It must be emphasized that the strength and permanence of this association depends on the simultaneous repetition of the adequate and conditioning stimuli and their mutual reinforcement, for the associations soon tend to disappear if the adequate stimulus fails. The restriction of the spread of a differentiated conditioned response from other parts of the cortex may be explained as due to the tonic inhibitory influence which the other parts of the cortex exercise over the zone surrounding the excited area (area of negativity).

Active Internal Inhibition. The conditioned response will soon cease if it is repeated without being combined with the adequate stimulus. Pavlov explains this as due to inhibition of an active kind. Also Sherrington, Forbes, and Beritoff consider this **internal inhibition** as an active dynamic neurogenic process. It develops and passes off and like excitation it irradiates rapidly from its primary focus (of an indifferent or inactive stimulus) into other parts of the cerebral cortex. It is known that the pyramidal tracts, the tectal-spinal tracts, the cerebellar cortex and other superimposed centers and tracts exercise a similar tonic inhibition on the reflex centers. This active internal inhibition is a conduction phenomenon which requires the passage of a nerve impulse, the discharge of nerve fibers, cells and synapses. It may last indefinitely, for minutes and even hours and may produce a profound depression of the cortex analogous to **hypnosis.** This depression may present a resemblance to sleep, but it is in fact a dynamic phenomenon due to a process of active inhibition. It tends to become weaker with lapse of time.

If a salivary reflex response is evoked from stimulation of two points on the skin and then one of these points is made inactive, then a stimulus applied to the inactive point will fail to evoke flow of saliva but stimulus from second point will evoke it easily if it is applied immediately after the first inactive one, — the two summate. If applied later (5 sec.) it is a little weaker, much weaker if applied 15 seconds later and entirely inhibited if applied 20 seconds later (by spread of inhibitory influence of the first). After an interval of 60 seconds when the inhibition of the first inactive stimulus has worn off the second point will evoke the response full strength. Take a series of four active spots and one inactive on skin of hind leg. Stimulation of each of the upper four for 30 seconds is accompanied by ten drops of saliva, while stimulation of the fifth produces none. If the inactive spot is stimulated first, within 30 seconds stimulation of any one of the other four spots is inactive due to spread of inhibition from first inactive stimulus. After one minute activity of these spots begins to appear in order from above down, 5, 3, 1, 0 drops of saliva; after two minutes 10, 8, 5, 2 drops of saliva; after four minutes 10, 10, 10, 4 drops of saliva; after six minutes 10, 10, 10, 10 drops of saliva. Inhibition spreads over a wide area of the analyzer and is diminished first in the areas most distant from the inactive or inhibitory spot.

If a number of various stimuli have been made active for secretion of saliva they will also act when combined (summation). But if one of them is made feeble by inhibition, the others are also inhibited if tested at once. After several minutes the activity will return to all except the first one inhibited and later that will return.

If the sound of a bell is not at once followed by the presentation of food but after two minutes, after sufficient repetitions this becomes a conditioned response. The secretion of saliva will follow two minutes after a stimulus. It is clear that the effect of the stimulus must persist in the center but is an inhibition which as it subsides allows the secretory response to emerge. That this is true can be shown by the application of some indifferent stimulus during the interval (of 2 minutes) when the saliva will appear at once. This is **inhibition of inhibition.** That is, one inhibitory process may stop a previous inhibitory process and if it happens to coincide in time with some other excitatory process will combine or summate with it and make the response come off.

A stimulus made to evoke a salivary response may be abolished by removal of a part of the frontal cortex but it may retain its ability to inhibit other active stimuli which shows that the inhibition is exercised on the other analyzer and not on the motor center.

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PHYLUM CHORDATUM

HEMICHORDA — Enteropneustans (Balanoglossus)
UROCHORDA — Tunicates or Ascidians (Molgula)
CEPHALOCHORDA — Lancelets (Branchiostoma)
VERTEBRATA —
  Cyclostomata — lampreys and hags
  Elasmobranchii —
    Selachii — shark, rays
    Holocephali — chimaeras
  Pisces —
    Dipnoi — lung fishes (Neoceratodus, etc.)
    Crossopterygii — lobe fins (Polypterus)
    Ganoidei — ganoids (Amia, Acipenser, etc.)
    Teleostei — bony fishes
  Amphibia —
    Urodela — salamanders
    Anura — frogs, toads
    Apoda — caecilians
  Reptilia — reptiles
    Lacertilia — lizards
    Ophidia — snakes
    Rhynchocephalia — tuataras
    Crocodilia — crocodiles
    Chelonia — turtles
  Aves — birds
    Ratitae — ostriches, apteryx and moas
    Carinatae — all other birds
  Mammalia — mammals
    Prototheria — Ornithorhynchus — Echidna
    Metatheria — pouched mammals
      Polyprotodontia — opossums, bandicoots, etc.
      Diprotodontia — kangaroos, wallabies, wombats, etc.
    Eutheria — placental mammals
      (For orders of mammals see page 9)

This classification was provided by Professor H. D. Reed.

PART III

BRAINS OF LOWER VERTEBRATES

CHAPTER 34

THE BRAINS OF REPTILES

IN the turtles the brain does not fully occupy the brain case, as if the brain were reduced in size. This condition resembles that seen in most Fishes. As a result the brain case can be easily opened without injuring the brain and the cranial nerves will be found to be greatly elongated within the brain case and can be readily traced to their exits. The pia, richly supplied with blood vessels, closely surrounds the brain. In other Reptiles such as Lizards (fig. 220) and Snakes the size of the head is small and the brain case fits more closely around the brain.

The Reptilian brain is narrow and elongated. The forebrain, midbrain and hindbrain segments are readily recognized. The elongated **forebrain** behind the olfactory bulbs possesses a distinct cortex and surrounds a small **thalamus** with which it is in intimate fiber connection. Its interior is occupied by greatly enlarged striatal structures (fig. 219) that resemble those of the Mammals. These are connected with the thalamus by large fiber tracts. The roof of the thalamus is projected dorsally as a dorsal sac, between the forebrain hemispheres. In the Lizards it is connected with a vestigial median eye lodged in the cranial roof. The **midbrain** has well-developed optic lobes or **tectum** in which the optic tracts (*ot*) end. Behind the tectum is a rudimentary median **cerebellum** which is best developed in swimming forms. The cerebellar brachia are likewise insignificant. The sluggish life and cold blooded nature of the Reptiles must be kept in mind in this connection. In spite of this the forebrain is much larger than in Amphibia and its thalamic and striatal structures are more highly developed. The oblongata or bulb is elongated and has a distinct ventral curve like that of the Mammals. Its membranous roof (*chp*) is overhung by the caudal curve of the median cerebellum.

The cranial nerves of Reptiles, twelve in number, correspond to those of Mammals (fig. 216).

1. The **olfactory nerves** (*oln, aon*) arise from cells in the small nasal sacs. In most other Vertebrates they are short filaments and enter the olfactory bulb directly through the cribriform plate. In the turtle they are greatly elongated round cords that pass back for a considerable distance within the brain case to end in the olfactory bulbs (*ob*). Two divisions of the olfactory nerves are seen: the ventral lateral division (*oln*) is larger and enters the ventrolateral part of the olfactory bulb. The dorsomedial division (*aon*) is smaller and enters the corresponding part of the bulb.

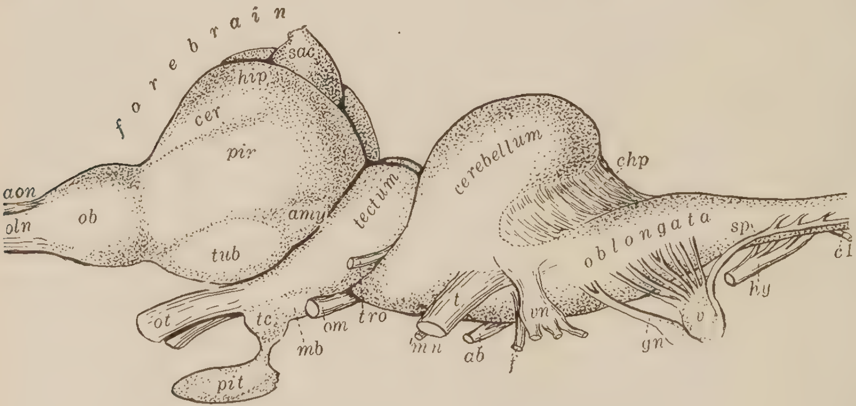

FIG. 216. Brain of green turtle, *chelone mydas*, left side, × 1½.

These two divisions appear to correspond to the Mammalian structures (fig. 180). The true olfactory nerve (*oln*) is markedly reduced in these aquatic reptiles in whom the ethmoidal turbinates are also insignificant. The accessory olfactory nerve (*aon*) is relatively large, probably due to the larger vomeronasal structures with which it is connected. The **olfactory bulbs** (*ob*) form the tips of the forebrain hemispheres of which they are forward extensions containing an extension of the ventricle in their interior (fig. 221). A constriction, the coronal sulcus, marks the junction of the bulbs with the forebrain.

2. The **optic tracts** (*ot*) that come from the retinæ of the eyes are well developed. They enter the cranium together and pass backward to decussate in front of the hypothalamus. Passing around the hypothalamus they end in the large vesicles that form the tectum of the midbrain.

3. The **oculomotor nerves** (*om*) spring from the ventral surface of the midbrain back of the hypothalamus and pass forward on each

side of it to enter the orbit. There they supply the recti muscles of the eye.

4. The **trochlear nerves** (*tro*) spring from the cleft between the cerebellum and tectum and pass forward over the side of the tectum to enter the orbit where they supply the superior oblique muscles.

5. The **trigeminus nerve** (*t*) whose peripheral branches supply the sensory fibers to the entire facial region arises from large trigeminal ganglia situated in the lateral cranial wall. The nerve (*t*) as seen in the brain case is formed by root fibers that come from the ganglion. The trigeminal nerve enters the side of the oblongata where it ends. The **masticator nerve** (*mn*) is a small filament on the ventral side of the trigeminal root. It comes from a motor nucleus in the pontal region. It supplies the muscles of the lower jaw.

6. The **abducens nerves** (*ab*) are small motor nerves. They spring from the ventral side of the bulb in the pontal region and extend forward to their exits. They supply the lateral rectus muscles of the eyes.

7. The **facial nerve** (*f*) is a small motor nerve which springs from the bulb ventral and in front of the large acoustic root. It passes out to supply the muscles of the hyomandibular region. The platysma and facial muscles are not developed in the Reptiles.

8. The **acoustic nerve** (*vn*) is a large sensory nerve that supplies the vestibular organ (fig. 217). It arises from a ganglion in close relation to the vestibule. Its root enters the acoustic region of the oblongata. In the Reptiles the lagena which is the forerunner of the cochlea is still a small structure and the cochlear division of the acoustic nerve is small, and the acoustic tubercle and trapezoid body are also small structures.

9. The **glossopharyngeal nerve** (*gn*) is a small mixed root just caudal to the acoustic. It joins the vagus to supply the pharynx.

10. The **vagus nerve** (*v*) joins the oblongata by a number of small rootlets in series with the glossopharyngeal (*gn*) and spinal accessory (*sp*). The three nerves together pass through the jugular foramen where the first two have sensory ganglia. They are mixed nerves consisting of motor and sensory fibers.

11. The **spinal accessory** (*sp*) is a motor nerve that springs from the lateral surface of the lower oblongata and cord. It passes upward to the jugular foramen to join the vagus with which it supplies the pharynx and œsophagus.

12. The **hypoglossus** (*hy*) are also motor nerves. They spring from the ventral surface of the lower oblongata and pass together forward through the base of the brain case to supply the tongue muscles.

A **median section** of the brain of the green turtle (fig. 218) shows the ventricular cavities within the brain and the thin incompletely developed brain walls which in their stage of development resemble the conditions seen in the fetus and young of Mammals. The fourth ventricle is a narrow elongated space roofed by the backward arch of the median cerebellum. The floor is formed by the dorsal surface of the oblongata. Each lateral wall is formed by the posterior medullary velum in which the choroid plexus (*chp*) is seen. The position of some of the nuclei and roots of the cranial nerves are shown as projected on the median surface.

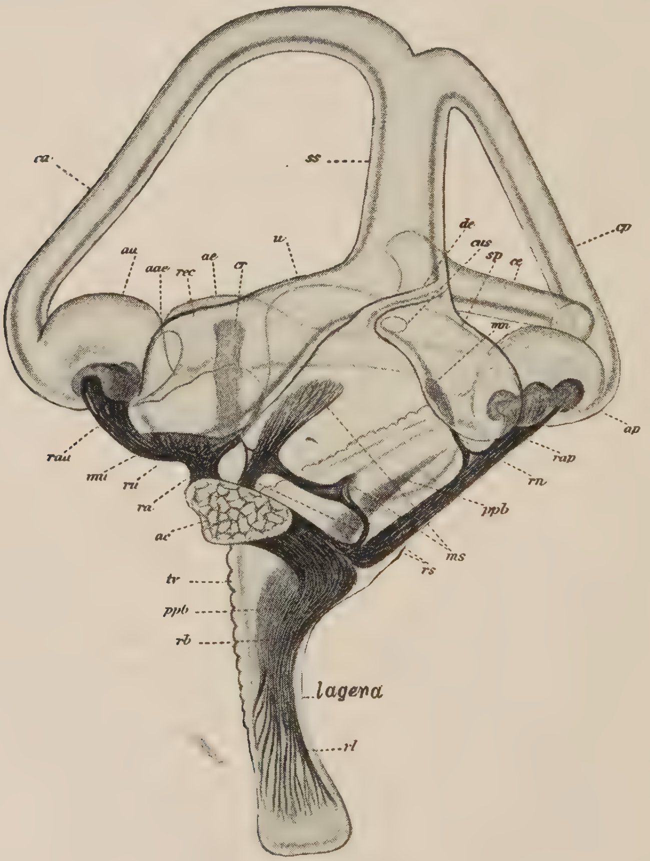

FIG. 217. Vestibule of an alligator. From Retzius.

On each side the cerebellar crest is connected with the bulb by a fibrous inferior peduncle (*rb*) just dorsal to the trigeminal root. On the ventricular surface a ridge connects the cerebellar peduncle with the floor of the midbrain.

The **optic lobes** (or tectum) appear as separate lateral evaginations from the cerebral aqueduct. They are joined together by a narrow median commissure (*csc*). Just in front of the optic lobes the pretectal regions of the thalami are united by a more conspicuous posterior commissure (*pc*). The floor of the midbrain or tegmental region is a thick fibrous plate that ends at the mammillary bodies (*mb*). The nuclei of the oculomotor (*om*) and trochlear (*tro*) nerves are situated in the tegmentum. The trochlear nerves pass dorsally to cross in the membrane which joins the cerebellum to the tectum. The inferior colliculi are too small to be recognized on the surface. In some Reptiles a tubercle formed by the inferior colliculus is seen in the posterior wall of the optic lobes, similar to that found in Birds and Amphibians.

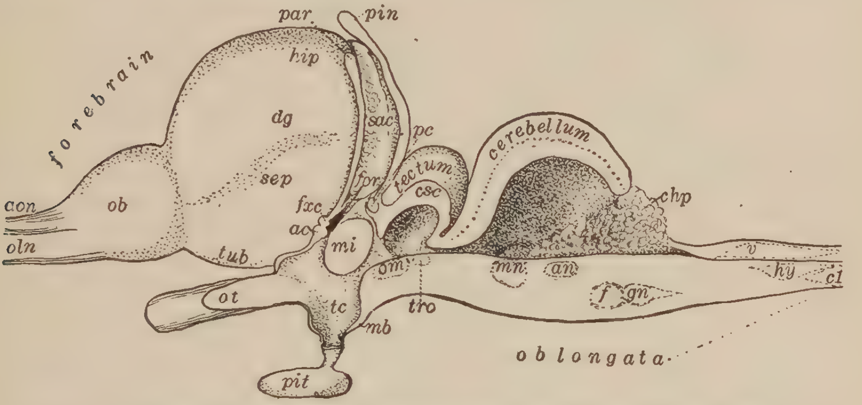

FIG. 218. Brain of green turtle, *chelone mydas*, medial view of right half, × 1½.

The **thalamus** of each side forms the lateral wall of the third ventricle, but is united with its fellow to form the massa intermedia (*mi*). The ventral or **hypothalamus** forms a prominent tuber (*tc*) between the optic tracts and over the chiasma (*ot*). The mammillary body (*mb*) forms a thickening in the back of the tuber. A narrow stalk connects forward with the pituitary body (*pit*) or hypophysis which is lodged in a fossa in the floor of the brain case.

The **somatic thalamus** forms the dorsal thicker parts united across the third ventricle by the massa intermedia (*mi*) or soft commissure. The somatic thalamus is in direct continuity with the tegmental region of the midbrain. Thick ridges formed by the medial and lateral forebrain bundles (figs. 235, 236) lead from the hypothalamus and somatic thalamus, one into the medial (septal) wall and the other into the lateral (striatal) wall of the forebrain. The pretectal portions of the thalamus are connected by the posterior commissure. The dorsal border is formed by the medullary stria (*oh*) and habenular nuclei (*hb*). The membranous roof that unites the thalamic masses forms, with the pineal body (*pin*), a dorsal sac between the forebrain vesicles. The small paraphyseal fold (*par*) occurs in front of the dorsal sac along which is seen a narrow choroid plexus. The third ventricle communicates laterally through the interventricular foramina (*for*) with the lateral ventricles of the forebrain hemispheres.

The **forebrain hemispheres** are laterally evaginated vesicles. Their ventricles communicate with the third ventricle. Their thick basal and lateral walls join the thalamus. Their medial walls are united by a thin terminal lamina through which the anterior (*ac*) and septal (or fornix) commissure (*fxc*) pass. The dorsal part of the lamina is drawn upwards with the dorsal sac forming a narrow diverticulum, the paraphysis (*par*). The thin medial wall bordering the terminal lamina is inturned into the lateral ventricles together with blood vessels to form the lateral choroid plexus. Through the terminal lamina in the region of the paraphyseal pouch a small posterior pallial commissure (*hc*) is formed in many Reptiles with well-developed hippocampal and piriform areas. It has been shown that this is the forerunner of the hippocampal commissure of Mammals (fig. 175, *hc*) formed by fibers of the angular bundle (*ang*) coming from the alveus and the piriform lobe. The fornix (dorsal or septal) commissure (*fxc*) is quite another structure and occurs in the septal region in relation to the anterior commissure (*ac*) which unites the amygdalar regions.

The **medial walls of the forebrain hemispheres** are formed of two parts separated by a thin area. The dorsal border is the hippocampal formation (*hip*). The thin region that blends with the dorsal margin is the dentate gyrus (*dg*). Ventral to the thin area is the septal region. It is seen to be connected (fig. 235) by a broad band of olfacto-septal and septohippocampal fibers which course in its medial surface. Bordering the terminal lamina just around the front of the interventricular foramen is a thicker band of fibers, the fornix, whose fibers cross in the midline and turn back into the hypothalamus. The fornix forms the small septal or fornix commissure (*fxc*) just in front of the foramen where it enters the septum. This is the septal commissure. In other Reptiles in whom the septal regions are thick the fornix (or septal) commissure is a large structure and unites the septa to a greater extent.

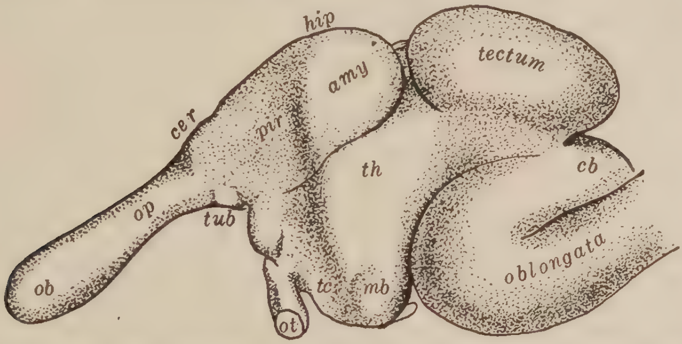

FIG. 219. Brain of a fetal gecko (lizard) of 7 mm. head length, lateral view, × 20.

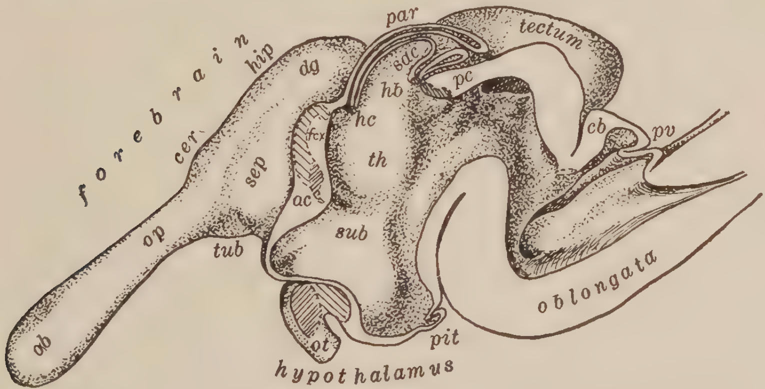

FIG. 220. Brain of fetal gecko, medial view of divided brain, × 20. From Tandler and Kantor.

In the medial wall of the forebrain there is seen another wide band of fibers on the ventricular surface, the alveus (*alv*), which come from the dentate gyrus (*dg*) and hippocampus (*hip*). Others from the amygdala (fig. 216, *amy*) and piriform area (*pir*) form the angular bundle. In many Reptiles these fibers decussate and form the prominent posterior pallial commissure (*hc*) in the region of the paraphysis.

Compare the brain of the mural lizard (figs. 219, 220, gecko) with that of the turtle or snake. The septal or anterior pallial commissure (*fxc*) is large and occupies a position in front of the amygdalar commissure (*ac*). A distinct dorsal position of this commissure is realized in mammals.

The anterior commissure (*ac*) is found in the ventral part of the terminal lamina. The two commissures can be easily distinguished (fig. 231). Fornix fibers (*fx*) coming through the septal region cross to form the septal commissure (*fxc*) and turn down to enter the hypothalamus as in amphibians. This system is the forerunner of the fornix longus and anterior pallial commissure (*fxc*) of Mammals. The other commissure (*ac*) is much the larger and unites the epistriatum or amygdalae and lateral olfactory regions of the two sides. Its connection forwards with the olfactory bulbs is very small. In Reptiles the amygdalar eminence (*amy*) is large and has been called the nucleus sphericus or epistriatum. It corresponds to the epistriatum of Fishes.

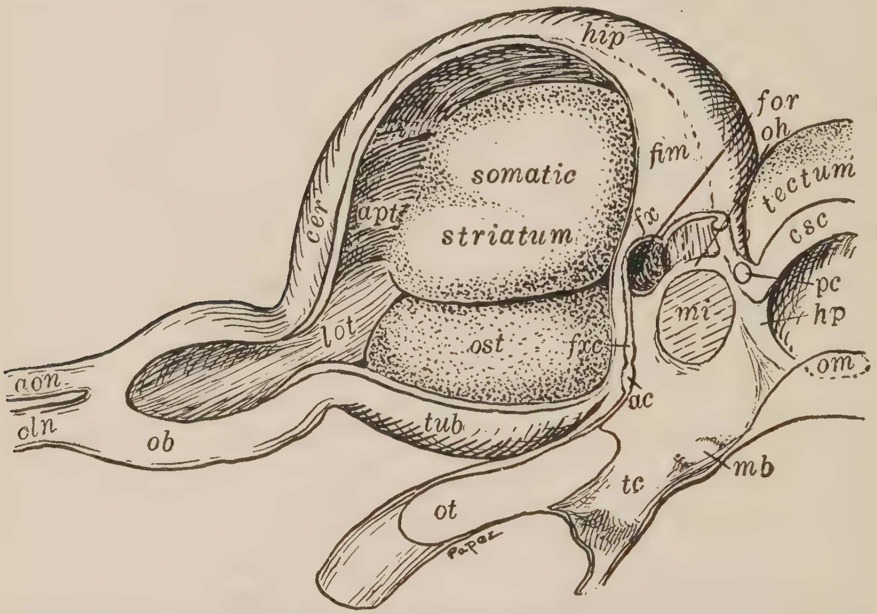

FIG. 221. Brain of green turtle. The medial wall of the right hemisphere has been removed to show the striatal eminences. The dorsal sac and pineal body have been cut away to expose the posterior medial wall, × 3.

When the medial wall of the forebrain is cut away the large lateral ventricles are found occupied by the lateral choroid plexus. This and the dorsal sac have been cut away in figure 221. There are now visible in the floor and lateral wall the striatal eminences, the olfactory striatum (*ost*) over the region of the olfactory tubercle (*tub*) and the sensory somatic striatum in the ventrolateral wall. At the caudal ventral pole the latter ends in the elevation formed by the amygdala (*amy*). A small band of thalamic radiations (*apt*) which pass through the somatic striatum is seen to enter the anterior lateral wall of the hemisphere (*cer*) just in front of the somatic striatum. For further description of the forebrain and its fiber connections see pages 406 and 503.

The **structure and fiber connections** of the Reptilian brain can best be studied in a series of cross sections. Most of the structures correspond to those seen in the Mammalian brain. The general plan of the fiber tracts is shown in figures 235 and 236.

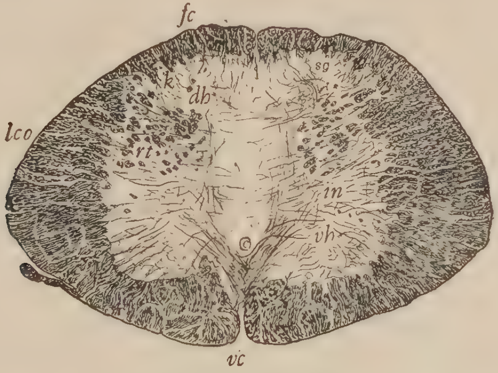

FIG. 222. Section of spinal cord of a water snake, *natrix sipedon*, × 25.

The **spinal cord** as seen in cross section (fig. 222) shows the *H*-shaped gray matter. A **dorsal** sensory (*dh*), a **ventral** motor (*vh*) horn are recognized, but there is a considerable amount of fusion of the gray columns. The dorsal, lateral and ventral fiber columns surround the gray. A large number of collaterals (*k*) are seen passing from the ventral and lateral fiber columns in to end around the large motor cells of the ventral horn. The intermediate region (*in*) of the gray is large in the snake and gives origin to a large ventral commissure (*vc*). The dorsal horns (*dh*) are covered by a substantia gelatinosa (*sg*) and are united by a commissure of fine fibers or collaterals. The small dorsal columns are formed by the entering dorsal (sensory) roots, numerous collaterals (*k*) coming from the dorsal columns enter the dorsal horn. From these a system of fine arcuate fibers pass ventrally through the gray matter and enter the lateral fiber column of the other side. They probably form the spinotectal and thalamic tracts. On each side the gray between the ventral and dorsal roots is invaded by a large bundle of scattered fibers that convert it into a reticular formation (*rt*). The indigenous tracts in the cord are the fasciculi proprii. The ascending tracts are the spinocerebellar (*dsc*), spinotectal (*st*) and spinothalamic (*sth*). The descending tracts are the vestibular tracts (*vs*), tectospinal tracts (*ts*) and rubrospinal.

A section through the lower **oblongata** (fig. 223) shows that the central canal (*c*) and the gray matter have shifted to a dorsal position. The dorsal horns are united over the canal, and form the primitive nuclei gracilis and cuneatus (*cn*) which emit the arcuate fibers that curve around the canal and decussate in the midline to form the medial lemniscus (*ml*). On the dorsolateral surface is the descending root of the trigeminus ending in the diffuse gray matter medial to it, from which an extensive system of arcuate fibers passes ventrally to form the crossed trigemino-thalamic tract (*sth*) near the ventral midline. A cluster of large cells that form the hypoglossal nucleus (*hyn*) is seen in the center of the reticular formation. From the medial side of this the hypoglossal nerve (*hy*) passes out ventrally. Near the midline is a small cell nucleus (*in*). On each

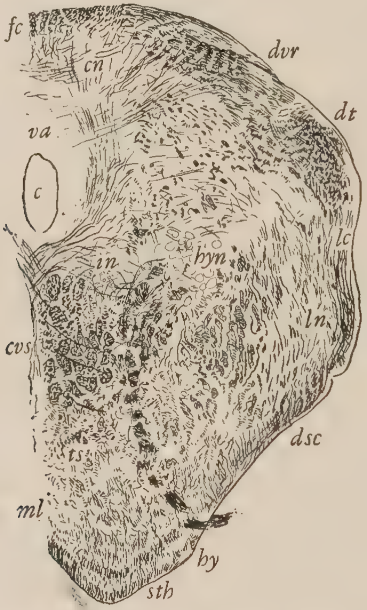

Fig. 223. Section of lower oblongata of a water snake, × 25.

side of the midline is the medial longitudinal bundle (*cvs*). The ventral lateral fiber columns of the cord at this level are interrupted by a diffuse nucleus of cells, the primitive lateral nucleus (*ln*) from which fibers pass laterally and upwards to the cerebellum.

A section above the obex (fig. 224) cuts through the entering vagal roots (*v*). Near the dorsal surface is seen the descending root of the vestibular (*dvr*) ending in relation to its descending nucleus (*dvn*). In the nucleus are seen fibers of the cerebellar bundle (*uf*) and many vestibular arcuate fibers pass ventrally into the reticular formation. The descending root of the trigeminus (*dt*) is seen just ventral to the vestibular, ending in relation to its large nucleus (*tn*). The vagal nuclei (*va*, *mv*) are found differentiated in the gray that forms the medial wall. The vagal roots (*v*) pass through the trigeminus root and nucleus to reach these. The dorsal vagal rootlets are sensory and form in the vagal nucleus (*va*) a diffuse descending tract (*sf*). The motor roots come from cells in the ventral part (*mv*). Cells in the lateral reticular formation form the ambiguus nucleus (*am*). Many fine arcuate fibers connect across the midline with the vagal nuclei and the ambiguus region. Arcuate fibers from the trigeminus nucleus (*tn*) cross through the reticular formation. In the ventral side is seen the inferior olive (*von*).

Sections through the upper end of the oblongata (figs. 225, 226) show in the dorsal lateral margin the entering vestibular nerve root (*dvr*) ending in relation to the large cells of the lateral vestibular nucleus (*lvn*). The vestibular root descends for a considerable distance ending in relation to its nuclei (*dvn*). From the vestibular nuclei arise two tracts of fibers. From the descending nucleus (fig. 125) arises a large tract that crosses the midline and descends as the crossed vestibulospinal tract (*cvs*) which forms the dorsal compact part of the medial longitudinal fasciculus. From the large cells of the nucleus at the level of the facial nerve (fig. 125) arises a tract of fibers (*vs*) which passes ventrally into the reticular formation of the same side. At the level of the masticator nucleus (fig. 126) another tract (*vm*) is seen to arise from the superior vestibular nucleus (*svn*) and to enter the medial longitudinal fasciculus in which it passes up to the trochlear (fig. 127, *tro*) and oculomotor nuclei (fig. 128). The abducens nucleus situated close to the midline (fig. 125, *an*) is intimately related to the vestibular arcuate fibers where they cross the midline.

Dorsal to the vestibular root is seen the root of the cochlear nerve (*nc*) entering the elevated acoustic tubercle (*at*). From the cells of the tubercle a fiber tract (*as*) passes to the midline with the vestibular fibers. These fibers cross in the midline in a more ventral position and pass upward on the other side as the lateral lemniscus to end in the inferior colliculus (fig. 227, *ll*, *ic*). In their course they accompany the spinotectal (*st*) and thalamic fibers from which they are distinguished by their internal position and by the fact that they end in the inferior colliculus. On its way the lateral lemniscus has associated with it a cluster of large cells, the primitive superior olive (*so*) and nucleus of the lateral lemniscus (*nll*), which gives origin to a commissure (*cll*).

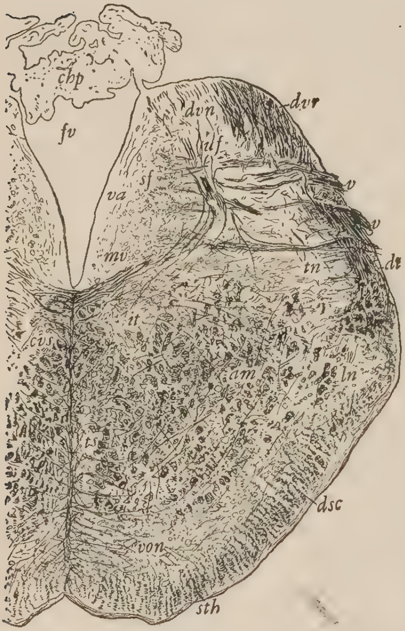

FIG. 224. Section through vagal region of a water snake, × 25.

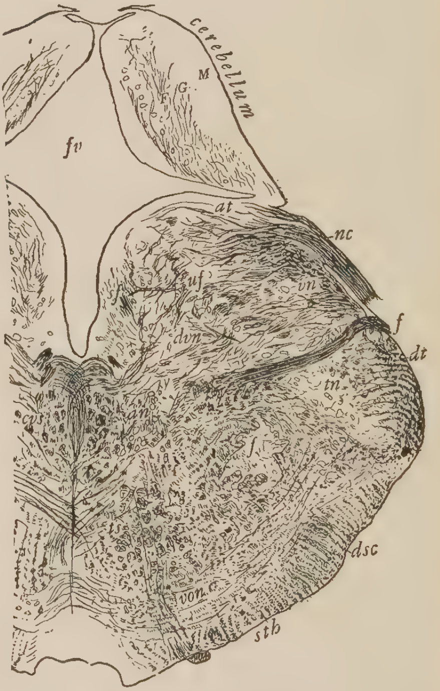

FIG. 225. Section through facial nucleus of a water snake, × 25.

The descending root of the trigeminus (*dt*) is seen ventral to the vestibular nerve root ending in relation to the trigeminal nucleus (*tn*). From the nucleus arcuate fibers are still seen passing ventrally to cross the midline and join the medial lemniscus (*ml*). The masticator (*mn*) arises from a large nucleus ventral to the trigeminus close to the nucleus of the facial.

The nucleus of the facial nerve (*f*) is another compact mass of cells seen medial to the trigeminus (fig. 225, *f*) and its outgoing nerve arises from its dorsal side and passes out on the lateral side.

The **fiber systems of the oblongata** form the medial longitudinal fasciculus, an outer fiber zone and a lateral reticular formation. The most distinct bundle seen along the midline is the medial longitudinal fasciculus. Its dorsal portion formed by vestibular fibers (*vm*) is most distinct and is seen to end in relation to the trochlear nucleus (fig. 127) and oculomotor nucleus (fig. 128). A similar descending bundle (*cvs*) passes down into the cord. The large tectospinal tract (*ts*) occupies a more ventral position near the midline. On the ventral surface near the midline are the large ascending sensory spino- and bulbo-thalamic tracts (*sth*). A large part of these are derived from the arcuate fibers of the trigeminus nucleus. More laterally are the spino-cerebellar tracts (*dsc*). Near the midline, especially in Reptiles that possess limbs, there is recog-

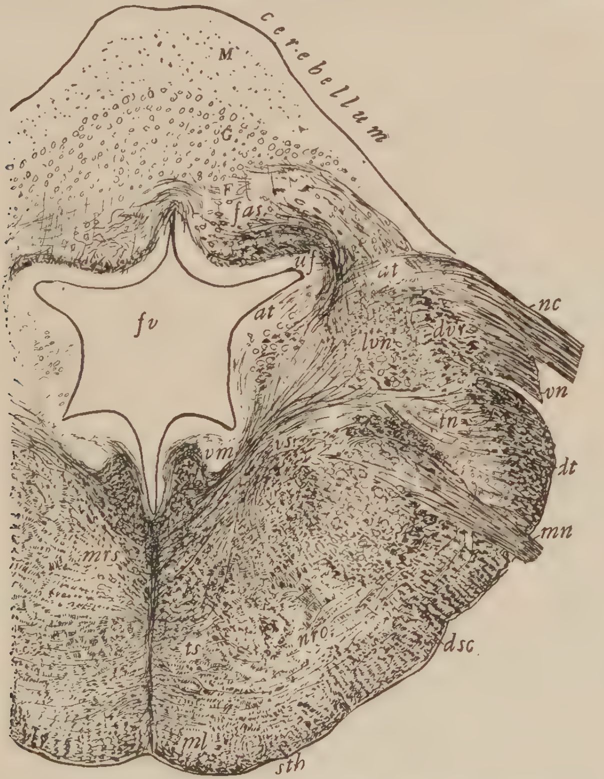

FIG. 226. Section through cerebellum and masticator nucleus, × 25.

nized the medial lemniscus (*ml*). It comes from the nuclei gracilis and cuneatus and ascends to the thalamus. This proprioceptive system is definitely formed in the Reptiles, though the Amphibians appear to have rudiments of it. A rubrospinal tract from the red nucleus descends through the reticular formation. The lateral lemniscus (*ll*) is formed of fibers that arise from the acoustic tubercle and pass medially and cross the midline with the vestibular tracts and pass up in the lateral side of the oblongata to reach the inferior colliculus (*ic*). Along their course are found clusters of cells that form the primitive superior olive (*so*) and nucleus of the lateral lemniscus (*nll*).

The **cerebellum** (*cb*) has a simple structure in the Reptiles. It consists of an outer molecular layer (*M*), a cellular layer (*G*), and a fibrous layer (*F*). The cellular layer is incompletely differentiated into Purkinje and granule cells invaded by a fiber layer. The deepest group of cells forms the primordium of the fastigial nucleus (*fas*). The more lateral part merges with the superior vestibular nucleus from which it appears to be differentiated. The cerebellum has three afferent and two efferent fiber tract connections. It is entered by the spinocerebellar tract (*dsc*) and a root of the vestibular nerve. These enter the granule layer and end there. Arcuate fibers from the inferior olive and lateral nucleus of the oblongata appear also to join these tracts and enter the cerebellum. Thus these afferent fibers to the cerebellum correspond to the restiform body (*rb*) of Mammals. Two tracts leave the cerebellum. A prominent bundle of fibers (*uf*) curves ventrally into the vestibular nuclei and descends through the descending vestibular nucleus (*dvn*) medial to the vestibular roots. It corresponds to a similar bundle seen in Fishes and Amphibians and to the uncinate fasciculus in the cerebellum of Birds and Mammals (fig. 150, *uf*). From the cells on the lateral side which is in large part the superior vestibular nucleus, a large bundle of fibers passes directly into the medial longitudinal fasciculus to the oculomotor nuclei. Other fibers from the more dorsal part appear to enter the reticular formation and form a true brachium conjunctivum (*bc*) which ends on cells in the reticular formation and on some large reticular cells (*rn*) in the region of the oculomotor nucleus. This primitive red nucleus gives off the rubrospinal tract. As compared with similar structures in Mammals, the brachium, red nucleus and rubrospinal tract are quite small and rudimentary in most Reptiles.

A more important connection is made by the uncinate fasciculus (*uf*) with the vestibular reflex centers.

The **structure of the midbrain** is shown in two sections (figs. 227, 228). Figure 227 is a section through the lower level that cuts the inferior colliculus (*ic*) and the trochlear nuclei (*tro*). The trochlear nuclei (*tro*) appear as conspicuous cell clusters in the gray matter, on each side of the aqueduct (*aq*). They receive a great quantity of fibers from the medial longitudinal fasciculus (*vm*, *ts*). From their lateral sides come the trochlear nerves which pass dorsally and cross in the roof in front of the cerebellum. In the lateral surface are seen the large spino- and bulbo-tectal tracts turning dorsally to enter the tectum as the prominent middle fiber stratum (*st*). Medial to this tract is the lateral lemniscus (*ll*) ending in the inferior colliculus (*ic*). In the lateral lemniscus are seen cel-

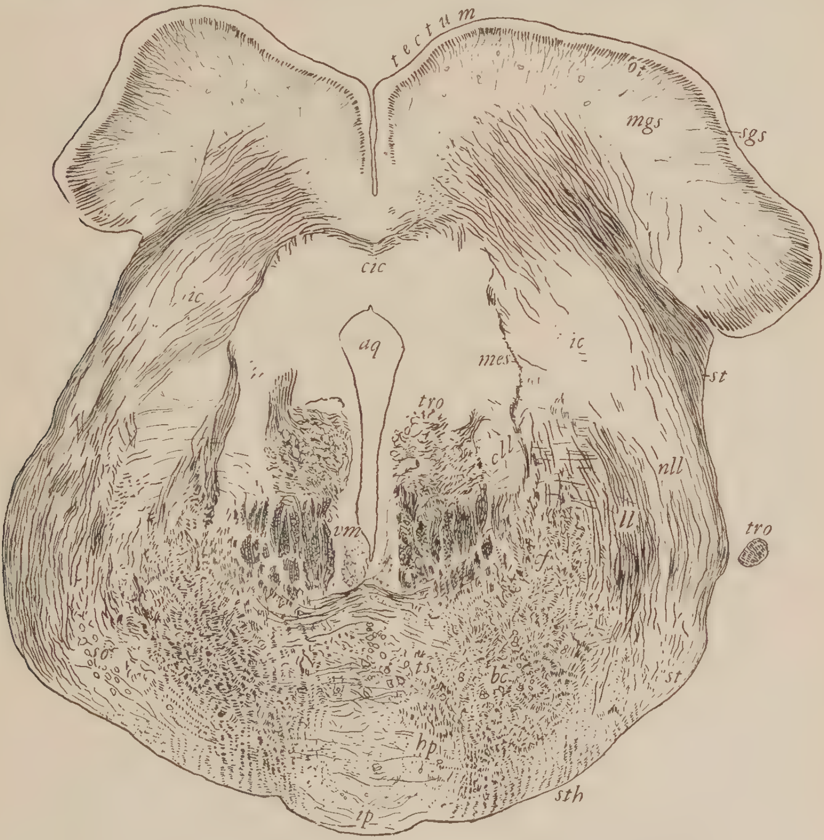

FIG. 227. Section through trochlear nucleus and inferior colliculi, × 25.

lular masses (*nll*) which give rise to commissural fibers (*cll*) that pass medially and cross the midline over the vestibulo-mesencephalic tracts (*vm*) and in front of the trochlear nuclei to end in the inferior colliculus of the other side. From the inferior colliculus fibers pass laterally to form a band on the outer surface (fig. 228, *bic*). This leads forward over an enlargement on the thalamus which may be considered as the primitive medial geniculate (*mg*) body of Mammals. Many of these fibers also cross back of the optic chiasma forming the geniculate commissure (fig. 235, *gc*).

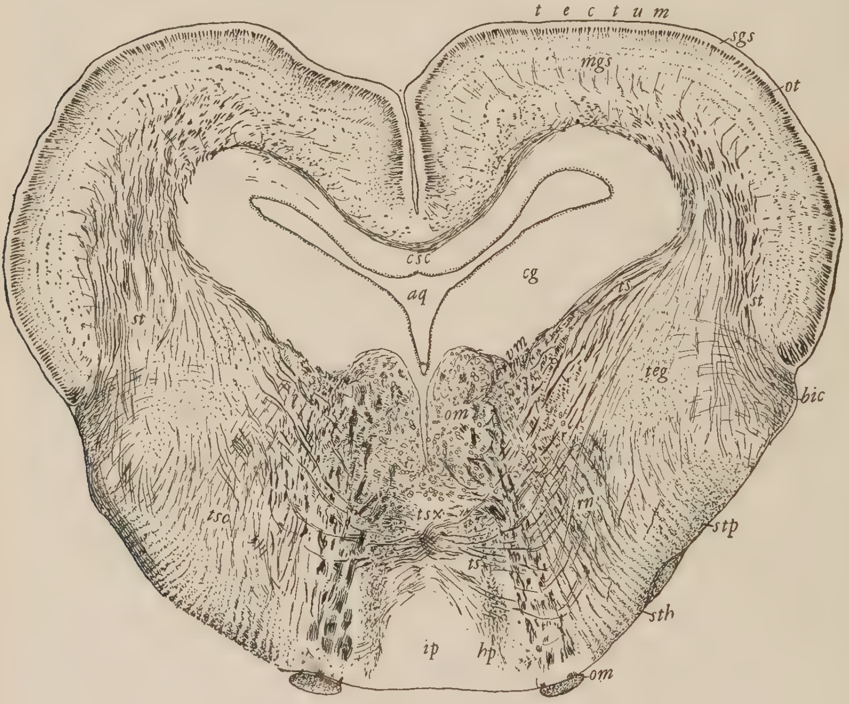

FIG. 228. Section through tectum and oculomotor nuclei, × 25.

The **tectum** or optic vesicles (fig. 228) form the conspicuous enlargements of the roof of the midbrain. They are entered from in front by the optic tracts (*ot*) from the retina which form a complete optic stratum through the tectum. The outer surface is formed by a thin cellular layer (*sgs*) over the optic stratum. The third layer or middle gray stratum (*mgs*) is a thick fibro-cellular layer. The optic vesicles are by no means limited to optic sensibility for they are entered from below by the large spino- and bulbo-tectal tract (*st*). This forms the prominent fiber stratum that permeates the middle gray stratum for its entire length and ends in a mass of cells, the pretectal nucleus (*npc*) at the front end of the midbrain. The deep stratum of fibers that surrounds the gray matter arises from the gray layers (*sgs*, *mgs*) and curving around the central gray (*cg*) decussates ventral to the oculomotor nuclei to form the descending tectospinal tracts (*ts*) ventral to the vestibular tracts (*vm*). Many of these fibers also end in the oculomotor (*om*) and trochlear (*tro*) nuclei. Many also cross in the roof before they curve ventrally, thus forming the commissure of the tectum (*csc*). The structure of the tectum and the arrangement of fiber tracts is similar to that seen in Mammals.

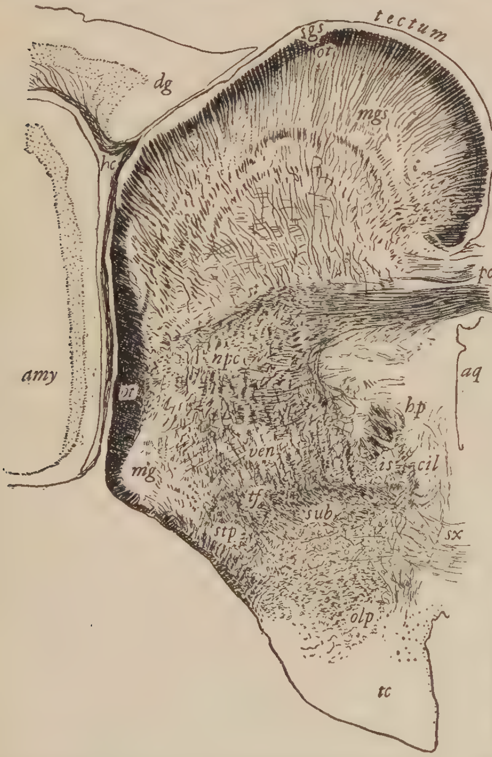

Fig. 229. Section through thalamus at posterior commissure, × 25.

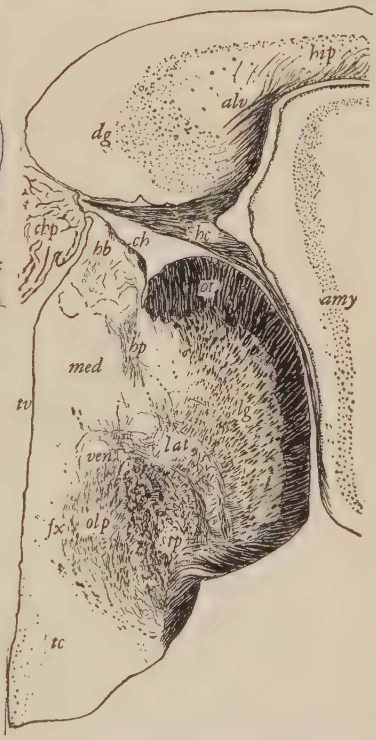

Fig. 230. Section through the middle of the thalamus, × 25.

The oculomotor nuclei (*om*) are large and conspicuously embedded in the medial longitudinal fasciculus (*vm*). They emit in a ventral direction the large oculomotor nerves (*om*). Ventral to the nuclei is seen the decussation of the tectospinal tracts (*tsx*) and on each side of the midline the tracts appear (*ts*). Ventral to these is the smaller habenulopeduncular tract (*hp*) seen ending in relation to the interpeduncular nucleus (*ip*). From the ventral surface lateral to the oculomotor nerves a system of fibers (*sto*) from the forebrain bundle (*stp*) is seen passing dorsally to the oculomotor nuclei. This region is occupied by a mass of scattered cells, the red nucleus (*rn*), which receives the brachium conjunctivum from below (*bc*). From the red nucleus a small rubrospinal tract arises, crosses the midline and becomes lost in the reticular formation.

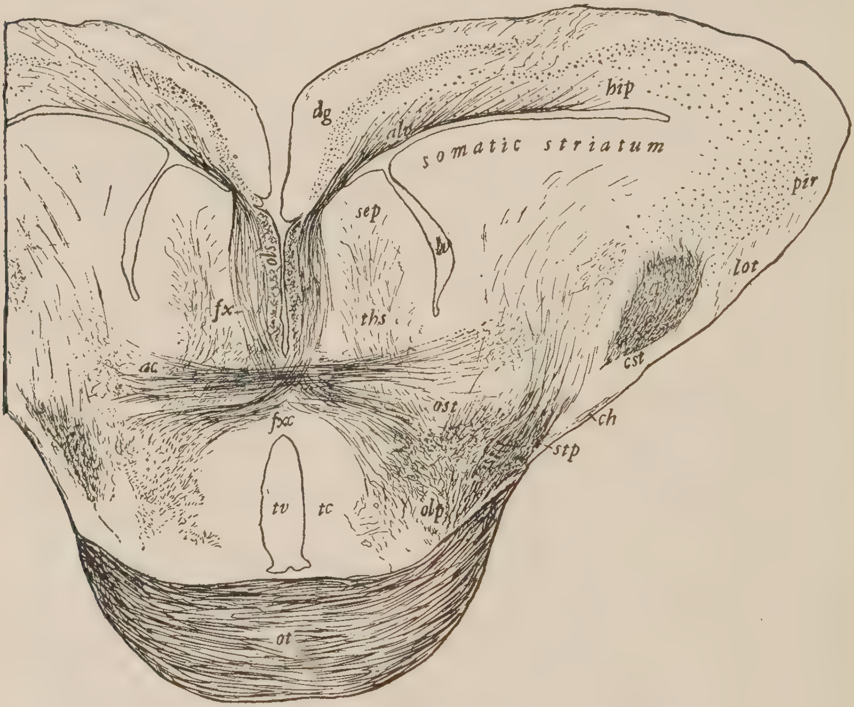

FIG. 231. Section through anterior forebrain commissures, × 25.

The tegmental nuclei (*teg*) are seen as diffuse cellular masses in the lateral part of the reticular formation. The forebrain bundle (*stp*) makes extensive connections with the ventral part (nucleus profundus mesencephali). The dorsal part receives fibers from the tectum and appears to contribute descending fibers into the ventral region.

The **structure of the thalamus.** A section through the posterior commissure (fig. 229) shows the extent to which the tectum extends forward over the thalamus. The habenulopeduncular tract (*hp*) is rapidly shifting dorsally to the habenula. Beneath the tectum is a diffuse cellular mass which may be designated as the nucleus of the posterior commissure (*npc*). It gives origin to the posterior commissure (*pc*). The nucleus receives the end of the spinotectal tract (*st*) and likewise fibers from the optic nerve. The fibers of the posterior commissure turn ventrally and caudally and end in the diffuse interstitial nucleus (*is*) and ciliary nucleus (*cil*) located orally to the oculomotor nucleus. Ventral to the nucleus of the posterior commissure are seen the spinothalamic tracts (*sth*) entering the posterior end of the thalamus. On the lateral side is the medial geniculate body (*mg*). It is continuous with the lateral nucleus of the thalamus as in Mammals.

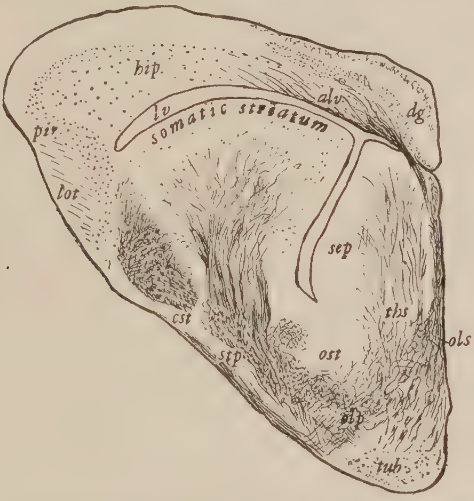

FIG. 232. Section through the middle of the forebrain, × 25.

The lateral forebrain bundle though small becomes more definite at higher levels (fig. 229, *stp*) and the medial forebrain bundle (*olp*) appears in the hypothalamus medial to it. The fibers that pass through the red nucleus end cephalad of it in a large nucleus comparable to the reticular subthalamic nuclei (*sub*) of Mammals. As in Mammals these nuclei are connected across the midline by a subthalamic commissure (*sx*) and the fiber stratum that is seen in them is comparable to that seen in Mammals. This fiber stratum gives rise to a large thalamostriatal tract (*tf*) which soon joins the descending striopeduncular tract (*stp*). Together they form the lateral forebrain bundle which extends upwards into the somatic striatum. Smaller groups of fibers (*apt*) from the medial, ventral and lateral thalamic nuclei and especially from the geniculate bodies, join the lateral forebrain bundle. Thus the bundle corresponds to the primitive (non-cortical) fibers of the Mammalian internal capsule. In figure 236 these components (*apt*, *tf*, *stp*) of the forebrain bundle have been separated.

A section through the middle of the thalamus (fig. 230) shows the extent to which the caudal pole of the forebrain overhangs the thalamus. The entire outer surface of the thalamus is covered by the large optic tract (*ot*), which encloses a large cellular mass, the lateral geniculate body (*lg*). This in the Reptiles is more nearly comparable to the nucleus of optic tract (*not*) of Mammals. The ventral part of the thalamus or the sub-thalamus contains the two forebrain bundles (*olp*, *stp*) side by side. The lateral (*stp*) contains a large group of ascending fibers from the thalamic nuclei. Medial (*med*), lateral (*lat*) and ventral (*ven*) nuclei are seen which contribute fibers into the forebrain bundles. Medial to the bundles, paraventricular nuclei are differentiated in the gray matter of the tuber (*tc*). At the dorsal border is seen the habenular nucleus (*hb*) and the corticohabenular tract (*ch*) ending in it. The habenulopeduncular tract (*hp*) seen in previous sections connects the habenular nucleus ventrally with the interpeduncular nucleus (*ip*). As the level of the anterior commissure is approached the corticohabenular tract loops laterally over the optic chiasma to enter the caudal surface of the forebrain from which it takes origin.

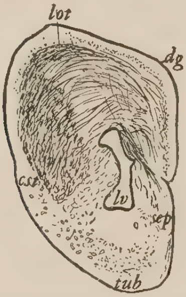

FIG. 233. Section through the front end of the forebrain, × 25.

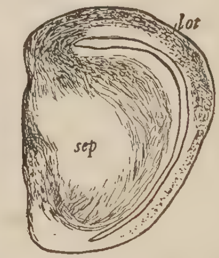

FIG. 234. Section through base of the olfactory peduncle, × 25.

The **structure of the forebrain** is shown in figures 229 to 236. A section through the caudal pole (fig. 230) shows that the lateral wall is thickened by a great internal bulging (*amy*) from which the large part of the anterior commissure (*ac*) takes origin. There are recognized an outer zone of large receptive cells in which the thalamic fibers end and a central mass from which the commissural fibers arise. A small part of this commissure has a frontal origin. The dorsal wall of the forebrain is formed by a thin general cortex, the medial wall of which forms the dentate gyrus (*dg*), and the dorsal wall the hippocampus (*hip*).

A section through the anterior commissure (fig. 231, *ac*) also cuts the optic chiasma (*ot*). The lateral forebrain bundle (*stp*) is entering the somatic striatum. This shows an outer border of cells in continuity with that of the piriform area (*pir*). A central and posterior group of cells gives origin to the middle division of the anterior commissure (*ac*). A large band of olfactory fibers, the cortico-epistriate tract (*cst*), is seen in the lateral wall ending in relation to the striatum. This (*cst*) is formed by the deep ventrolateral part of the lateral olfactory tract and is comparable to the external capsule (*e*) of Mammals. The more superficial part of the tract (*lot*) which ends in the piriform area (*pir*) is weakly developed and corresponds to the tract in Mammals. The piriform area (*pir*) contains a thickened plate of cells on the surface of which ends the lateral olfactory tract (*lot*). The dorsal wall is formed by a general cortex. As it approaches the medial border this cortex becomes the hippocampus (*hip*) with larger more deeply placed cells. The medial wall is the dentate gyrus (*dg*). It is formed by a plate of small cells. The connections of the hippocampus are best seen at the frontal end (figs. 232, 233). The olfactory fibers (*lot*) from the olfactory bulb are seen to enter the surface of the lateral wall and distribute to the general cortex. They curve

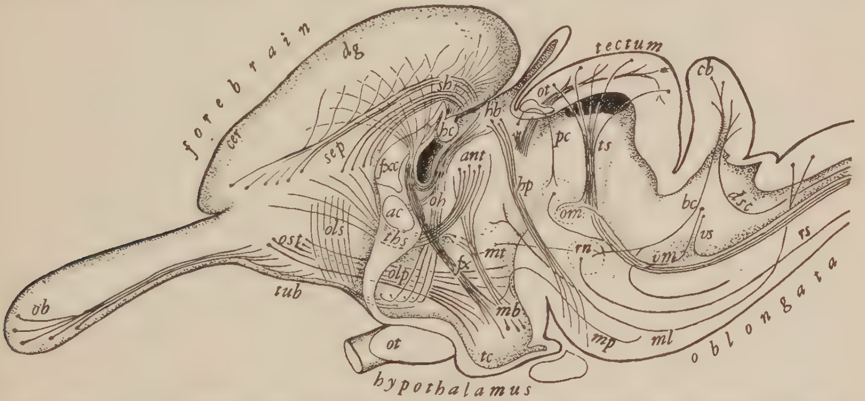

FIG. 235. Plan of fiber tracts of the Reptilian brain. Tracts are projected on the medial surface.

medially and enter also the surface of the dentate gyrus (*dg*). The dentate gyrus receives fibers mostly from the medial side. More caudally (fig. 231) large numbers of cortical fibers are added which give to the dorsal wall the semblance of a primitive general cortex. It seems likely that this area is also entered by ascending fibers from the lateral forebrain bundle. The ventricular surface of the dorsal wall is covered by a layer of fibers, the alveus (*alv*) which come from the cells of the dentate gyrus and hippocampus.

The septum (*sep*) is always sharply constricted from the dentate gyrus (*dg*) by sulci. Through this constriction the fibers of the alveus (*alv*) cross into the septum and pass in its medial or outer wall. They form the primitive fornix system. In the ventral part of the septum they decussate (fig. 231, *fxc*), pass laterally and turn caudally to form the medial part of the medial forebrain bundle (*olp*), with which they are distributed to the large cellular masses in the lateral wall of the hypothalamus (*tc*). These relations of the fornix fibers correspond closely to the conditions seen in the frog. They are also comparable to the fornix longus of Mammals. Most of these fibers pass ventral and in front of the amygdalar division of the anterior commissure (*ac*) but some pass dorsal to it and would represent the columns of the fornix as seen in Mammals.

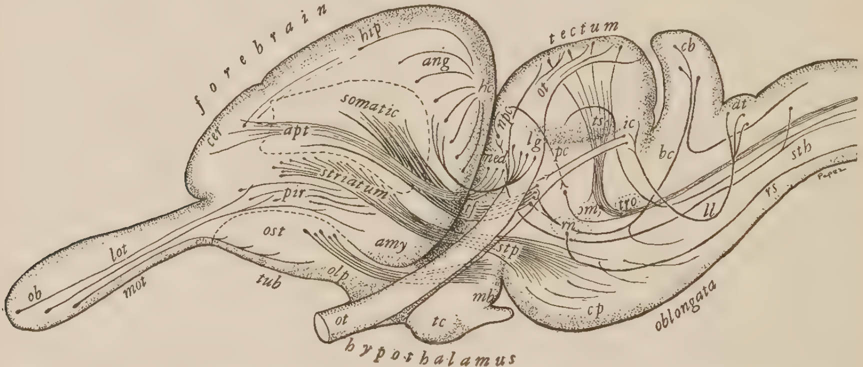

FIG. 236. Plan of fiber tracts of the Reptilian brain. Tracts are projected on the lateral surface.

In the medial (outer) surface of the septum are seen the olfacto-septal fibers (*ols*) coming in from the ventral and anterior region of the forebrain wall (fig. 234). In the inner or ventricular wall of the septum is seen the thalamoseptal tract (*ths*) that connects the dorsomedial region of the thalamus with the septum. Both these tracts (*ols, ths*) seem to be afferent to the septum, while fibers that join the fornix appear to be efferent ending in the hypothalamus (*tc*). Ventrally the septum joins the ventral olfactory area (*tub*).

The ventral wall of the forebrain (fig. 232) is a thickened area which forms the olfactory tubercle (*tub*). It receives from the bulb a diffuse tract of fibers (*mot*). Fibers from this region also enter the septum. The deeper portions that surround the ventricle are greatly thickened and form the anterior or olfactory striatum (*ost*). From this region a tract of fibers (*olp*) arises that passes down chiefly as the medial forebrain bundle. At the level of the commissures it is joined by the fornix and septal fibers, and together they end in the hypothalamus.

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CHAPTER 35

The Brains of Birds

The brains of Birds resemble most closely those of Reptiles from which they have been derived. This resemblance applies also to the structure of the head (fig. 237) and the distribution of the cranial nerves (fig. 238). The form and structure of the head and brain of Birds are remarkably constant in the whole class. The brain differs from that of the lower forms in its greater breadth and in the shortness of its base. Its most characteristic features are the great development of the striatum in the forebrain, of a median cerebellum and of large laterally placed optic lobes or tecta.

The **forebrain** is usually broader than long. It consists of two pointed hemispheres. Each is tipped in front by a rudimentary olfactory bulb (*ob*). The posterior part of the forebrain is broad. Its size is due entirely to the great development of the somatic striatum which completely fills the interior. The lateral ventricles and dorsal wall are small and displaced dorsally and enclose a small choroid plexus. On account of the atrophy of the olfactory nerve and bulbs, the hippocampal formation in the dorsal and medial wall is weakly developed. Where it joins the striatum on the dorsal surface a groove is often seen. The dorsal surface is convex and in many Birds it shows lateral prominences of the striatal body. The posterior poles, formed by the amygdalar division of the striatum, extend back over the thalamus and tecta. Wedged between them is a small pineal body and the large median cerebellum. A small anterior commissure connects the two amygdalar regions. There is no corpus callosum and the fornix system is vestigial. The ventral surface is concave where it lies over the large orbit. The region of the olfactory tubercle is much reduced. The striatum is a sensomotor correlation center. Its afferent connections are with the tectum and thalamus. Its three efferent paths reach the oculomotor, cerebellar and masticator centers of the brain.

The **thalamus** is short and small. Excepting the optic tracts (*ot*) which are of large size and cover its ventral surface, the thalamus is hidden from view. A small tuber cinereum (hypothalamus) is seen back of the optic tracts where it connects with the hypophysis. The thalamus is the chief internode through which the sensory systems connect with the striatum.

The **midbrain** presents two greatly enlarged optic lobes or tecta which are entered by the optic tracts. The optic lobes are laterally displaced by the median cerebellum and the tectal commissures are laterally stretched. Only in some bony fishes (Teleosts) does the development of the tectum equal that of Birds. The strong posterior bulging of the tectum is due to the presence of a large nucleus isthmi developed most highly in Birds. The afferent connections of the tectum are with the retina and the efferent are chiefly with the striatum. They form an important optico-sensory system. The interior of the midbrain contains the chief oculomotor centers and in addition the cerebellar rubro-spinal connections for locomotion and flight.

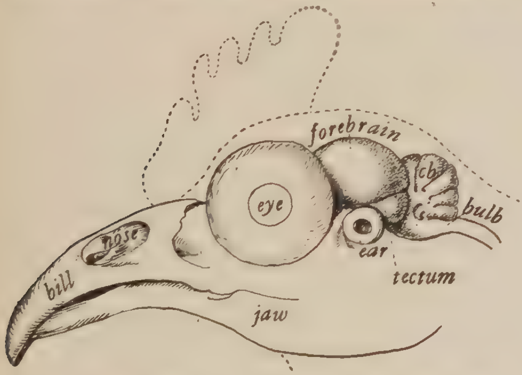

Fig. 237. Brain of a domestic fowl, left side—exposed from above to show its position in the head, × 1.

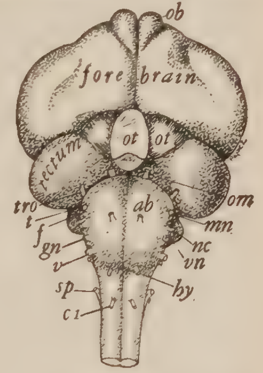

Fig. 238. Ventral view of brain of domestic fowl, × 1½.

The **cerebellum** is a median structure with well-developed transverse folia. An anterior, a middle and a posterior lobe are recognized. On each side there is a small lateral or floccular lobe. The median dorsal position of the cerebellum is like that seen in higher Sharks. The deep cerebellar nuclei are closely connected with the vestibular centers. Spinocerebellar tracts, a restiform body and in some species a pons are recognized as afferent connections. Internal efferent connections are by means of the uncinate bundle with the vestibular centers, by the brachium conjunctivum with the red nucleus and thence by the rubrospinal tract with the motor nuclei of the cord. A special connection with the striatum exists. The cerebellum is thus connected with the tonic, static and kinetic systems of the brain.

The **oblongata** or bulb is greatly swollen by the large pontal, olivary and acoustic nuclei. There is a sharp ventral pontal flexure. On account of the smallness of the cerebellar connections and its median nature the walls of the oblongata show only a moderate degree of the lateral eversion which is so prominent in Mammals.

The cranial nerves (fig. 238) are quite like those of Reptiles (page 388). The hypoglossal (*hy*) is distinct from the cervical nerves. It supplies the tongue muscles and syrinx. The spinal accessory (*sp*) is small. The vagus (*v*) and glossopharyngeal (*gn*) are distinct and supply the viscera. The taste nerves and centers are rudimentary. The vestibule and vestibular nerve (*vn*) and its centers are highly developed. The facial (*f*) is small and supplies the constrictor colli and depressor mandibulae muscles. The abducens nerve (*ab*) is distinct and supplies in addition to the lateral rectus the special muscles in the orbit. The trigeminus (*t*) is reduced in most Birds owing to the reduced sensory function of the bill. In water birds with a sensory bill it supplies the special sensory endings. The masticator nerve (*mn*) supplies the adductor muscles of the mandible. The trochlear nerve (*tro*) comes from the dorsal side of the isthmus and supplies the superior oblique muscle of the eye. The oculomotor (*om*) with the ciliary fibers comes from the ventral side of the midbrain and supplies the remaining eye muscles. The eyes and optic nerves are large. The nerves cross and each enters the opposite tectum which forms the dominant sensory system in Birds. The olfactory nerves (*oln*) are rudimentary.

The **spinal cord of Birds** extends the entire length of the vertebral canal so that no cauda equina or terminal filum occurs. In the dove there are twelve cervical, eight thoracic, twelve lumbosacral and six coccygeal pairs of nerves. These connect with the cord by ventral (motor) and dorsal (sensory) roots. Like the bird's neck the cervical cord is long. The 9th to 12th segments are enlarged on account of their connection with the large nerves that supply the wings and pectoral muscles used in flying. The lumbosacral segments that supply the legs are also enlarged and their dorsal walls are splayed apart forming the rhomboid sinus. The following cross sections are drawn from a Weigert series of the brain of an American robin, *Merula migratoria*.

A section of the cervical cord (fig. 239) shows a typical *H*-shaped gray matter. The dorsal column of fibers (*fc*) formed by the dorsal root fibers of the cervical nerves ends by collaterals (*k*) in the substantia gelatinosa (*sg*) of the dorsal horn and by reflex collaterals (*k*) in the intermediate nucleus (*in*). The dorsal horn is made up chiefly of substantia gelatinosa (*sg*). The central nucleus is very small. From the substantia arcuate fibers pass ventrally to cross in the ventral commissure and form the spinotectal tract on the other side (*st*). The ventral horn (*vh*) contains a well-developed group of motor cells that give rise to the ventral root (*mr*) which supplies the neck muscles. In the cervical and lumbar enlargements the ventral horn is thrust laterally and contains another large lateral group of cells which supply the limb muscles. Those for the pectoral muscles are highly developed in birds that fly. Great quantities of collaterals (*k*) pass into the ventral horn from the surrounding fiber columns. A well-developed cluster of cells forms the intermediate nucleus (*in*). These cells receive collaterals from the dorsal columns (*fc*) and give rise to a large number of fibers that cross in the ventral commissure (*vc*) and become the ventral fasciculus proprius (*vp*) of the other side. In the cervical and lumbar enlargements a homolateral fasciculus proprius is also derived from the intermediate cells. The cells just adjacent to the substantia stand in relation to the reticular formation (*rt*).

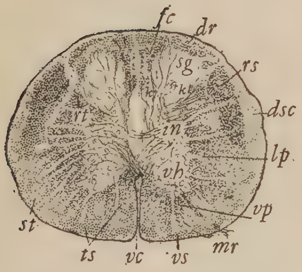

FIG. 239. Section of upper cervical cord of a robin, ×13.

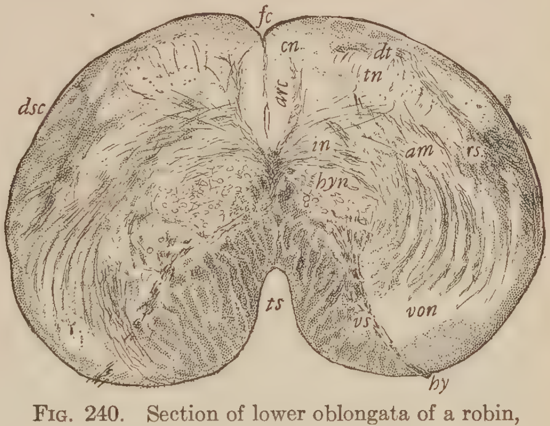

FIG. 240. Section of lower oblongata of a robin, *Merula migratoria*, × 13.

The **white matter** forms the dorsal (*fc*), lateral (*lco*) and ventral columns of the cord. It consists of nerve fibers surrounded by thin myelin sheaths. Those of the dorsal columns (*fc*) are of large caliber; those over the substantia (*dr*) are of fine caliber. The rubro-spinal tracts (*rs*) have fibers of large caliber, heavily myelinated. A zone (*rt*) of much finer fibers is situated on each side of the dorsal horn. The ventral horns are surrounded by the fasciculi proprii (*vp, lp*) or reflex bundles of the cord. On the surface are the large tectospinal (*ts*), vestibulospinal (*vs*), spinotectal (*st*) and spinocerebellar (*dsc*) tracts.

The **oblongata of Birds** (fig. 137), unlike that of Reptiles, possesses rudimentary pontal nuclei and pons which form a band over its ventral surface at its oral end. The cochlear and vestibular nuclei and tracts as well as their cerebellar connections are highly developed in Birds. The other cranial nerves have a typical Reptilian disposition.

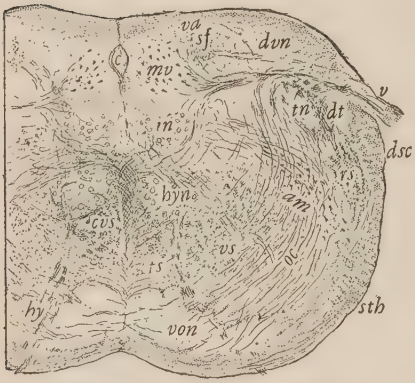

FIG. 241. Section of oblongata of robin, at obex, × 12.

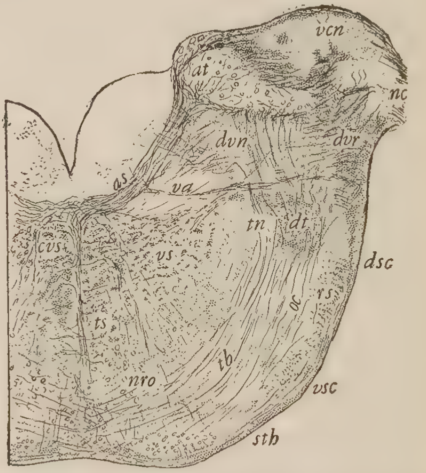

FIG. 242. Section of oblongata through cochlear nuclei, × 12.

A section through the lower end of the oblongata (fig. 240) cuts the **hypoglossal nucleus** (*hyn*). The nerve (*hy*) passes out ventrally to supply the muscles of the tongue and syrinx. The larynx of the Birds is voiceless. The nuclei lie against the medial longitudinal bundles which send into them quantities of collaterals. Overlying the hypoglossal nucleus is a large mass of smaller cells (*in*) and great quantities of fibers connect it with the medial longitudinal bundles. The ventrolateral fiber columns of the cord are interrupted by a large inferior olive (*von*). On the lateral side are seen the rubrospinal (*rs*) and spinocerebellar tracts. The dorsal fiber columns (*fc*) are ending in a small nucleus (*cn*) which is giving off arcuate fibers (*arc*) ventrally. The descending root of the trigeminal nerve (*dt*) is ending in an enlargement of the trigeminal nucleus (*tn*). This nucleus gives off a large number of arcuate fibers that curve ventrally into the region of the inferior olive (*von*). A large nuclear mass (*am*) is seen in the reticular formation lateral to the hypoglossus.

At a higher level where the oblongata begins to open (fig. 241) the roots of the **vagus** (*v*) are seen to enter the central gray dorsal to the canal. Sensory filaments form the solitary fasciculus (*sf*) which ends in relation to the sensory nucleus (*va*). Between this and the hypoglossal (*hyn*) is the motor vagus (*mv*) which gives origin to the motor filaments. More laterally in the reticular formation is the lateral vagal nucleus (*am*). The hypoglossal nucleus (*hyn*) is capped over by a special group of cells (*in*). From the inferior olive (*von*) a large number of olivocerebellar fibers (*oc*) pass dorsally through the descending root of the trigeminus.

A section through the middle of the oblongata (fig. 242) cuts the vestibular and cochlear nuclei which form the dorsolateral border. The cochlear organ in Birds is more developed than in Reptiles. The **cochlear nerve** (*nc*) enters the large angular nucleus (*vcn*) and passing over this ends in the lamellar nucleus (*at*) which is specially developed in Birds. These cochlear nuclei resemble those of some lower Mammals (marsupials), though their eversion over the border of the oblongata has not taken place. Ventral to the cochlear nucleus (*at*) are the descending vestibular nucleus (*dvn*) and root (*dvr*). Two streams of fibers leave the cochlear nuclei. From the lamellar nucleus (*at*) a large band (*as*) passes medially to cross the midline; a smaller number pass ventrally to the superior olive. This system resembles the acoustic stria of Mammals. From the ventral side of the lamellar and the angular nucleus (*vcn*) another stream of fibers (*tb*) passes ventrally through the vestibular nuclei (*dvn*), crosses the midline and reaches the superior olive (figs. 243, 244, *so*), around which it forms the lateral lemniscus (*ll*). This system (*tb*) corresponds to the dorsal or internal division of the trapezoid body of Mammals.

The **vestibular nerve** arises from cells in the vestibular ganglion. Its peripheral branches supply the end organs in the semicircular canals, saccule and utricle. The nerve (fig. 243, *vn*) enters the vestibular nuclei ventral to the cochlear. It extends downwards as the descending vestibular root (fig. 242, *dvr*). Great quantities of collaterals enter the vestibular nuclei. Three vestibular nuclei are recognized, a medial or descending (fig. 242, *dvn*), a lateral (fig. 243, *lvn*) and a superior (fig. 244, *svn*). From the medial nucleus (*dvn*) fibers pass across the midline and enter the medial longitudinal bundle in which they form the descending crossed vestibulospinal tracts (*cvs*) and the ascending vestibulo-mesencephalic tracts (*cvm*). From the lateral nucleus fibers pass (fig. 243, *lvn*) directly into the reticular formation and form the direct vestibulo-spinal tracts (*vs*) seen at lower levels. From the superior vestibular nucleus which consists of two parts fibers pass medially (fig. 244, *vm*) and turn upwards to reach the trochlear (fig. 245, *vm*) and oculomotor nuclei (fig. 246, *vm*). The vestibular nuclei are intimately connected with the cerebellar nuclei which send into them great quantities of fibers.

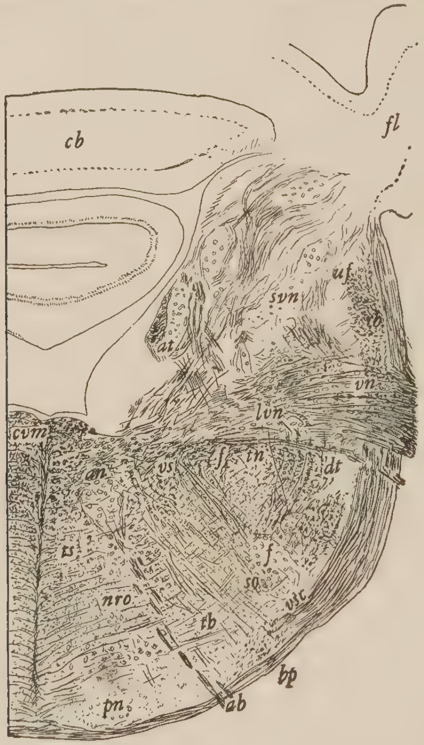

FIG. 243. Section through abducens and facial region, × 12.

The **facial nerve** (fig. 243, *f*) takes its origin from two groups of motor cells. The dorsal cell group is just caudal and ventral to the masticator nucleus. The ventral group is just lateral to the superior olive. Scattered cells connect the two groups. The nerve fibers curve dorsally and medially and then pass out laterally over the trigeminal root (*dt*) as in Reptiles. The fibers from the dorsal cell group supply the depressor muscle of the mandible. The ventral cell group supplies the constrictor colli muscle.

The **abducens nerve** (*ab*) arises from a large group of motor cells close to the dorsal medial line (fig. 243, *an*). It passes out ventrally and supplies the lateral rectus and retractor bulbae muscles of the eye.

The **masticator nerve** (fig. 244, *mn*) arises from a large group of motor cells ventral to the trigeminus. The nerve fibers pass out from its lateral surface and join the trigeminus (*t*). The nerve supplies the adductor muscles of the bill.

The **trigeminal nerve** (*t*) which supplies the sense organs in the bill and face in general is small in Birds in whom these structures and sensory areas are reduced. In the robin's brain the **trigeminus nerve** is small. It enters through the brachium pontis (fig. 244, *t*) and divides into a pontal and a long descending root. The descending root (*dt*) can be traced down through successive sections to the lower end of the oblongata (figs. 244 to 240). Along its medial side is a narrow column of cells, the trigeminal nucleus (*tn*), into which it sends numerous collaterals. From the nucleus arcuate fibers pass medially along the course of the olivocerebellar fibers (*oc*), cross the midline and enter the reticular formation.

The trigeminal nerve ends also by a short pontal root in the large pontal nucleus (fig. 244, *tn*). This nucleus gives origin to a large ascending tract which passes upwards to the thalamus. Wallenberg has described a crossed tract that ascends through the middle of the tegmental region and enters the striatum.

The **mesencephalic root of the trigeminus** as in other vertebrates takes its origin from the large globular cells in the medial border of the tectum (fig. 246, *mes*) and passes out between the trigeminus and masticator nerves to supply the sense organs of the mandibular muscles.

The **reticular formation** is rather extensive. It contains large scattered cells that constitute the reticular nuclei of the oblongata (*nro*) and at higher level of the pons (*nrp*). These cells give rise to fibers that pass dorsally, cross the midline and descend as the reticulospinal tracts, as in Mammals (fig. 153). The reticular pontal nucleus (fig. 245, *nrp*) is of great size in Birds and is intimately related to the decussation of the brachium conjunctivum (*bcx*).

The **cerebellum of Birds** is a well-developed median structure with a considerable number of folia. Small lateral or floccular lobes (*fl*) are present on each side. The folia and lateral surfaces are covered by a typical cortex. This consists of an outer molecular layer (*M*), a layer of Purkinje cells, a thick granular (*G*), and a central fiber layer (*F*). Within the fiber layer there are situated the cerebellar nuclei (fig. 244, *fas*, *nd*).

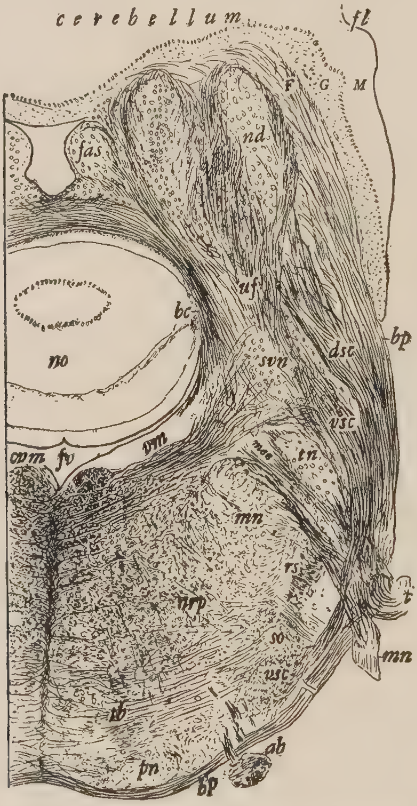

Fig. 244. Section through masticator and cerebellar nuclei, × 12.

The cerebellum is divided into anterior, middle and posterior lobes. The fissura prima (*fp*) that separates the anterior and middle lobes is near the dorsal anterior border. The pyramidal fissure is more distinct, and separates the posterior lobe from the middle. The anterior lobe is reached by the ventral, spinocerebellar tracts (*vsc*) of both sides. The posterior lobe is reached by the dorsal spinocerebellar tracts and vestibular fibers. The middle lobe and the flocculi are reached by fibers from the pontal nuclei. The large striocerebellar tract (*stc*) connects the cerebellar cortex with the paleostriatum (*ost*). A small tract of fibers (fig. 245, *bip*) passes from the nucleus isthmi down to the lateral part of the pontal nucleus.

The pontal nuclei (figs. 243–245, *pn*) are large irregular cell masses. Aside from the small tract (*bip*) the afferent connections of the pontal nuclei appear to be fine fibers from the surrounding reticular formation. A definite tract of fine fibers is seen on each side of the midline. The nuclei give origin to fibers that form in the robin a distinct band (*bp*) on the surface which enters the lateral or floccular lobes of the cerebellum.

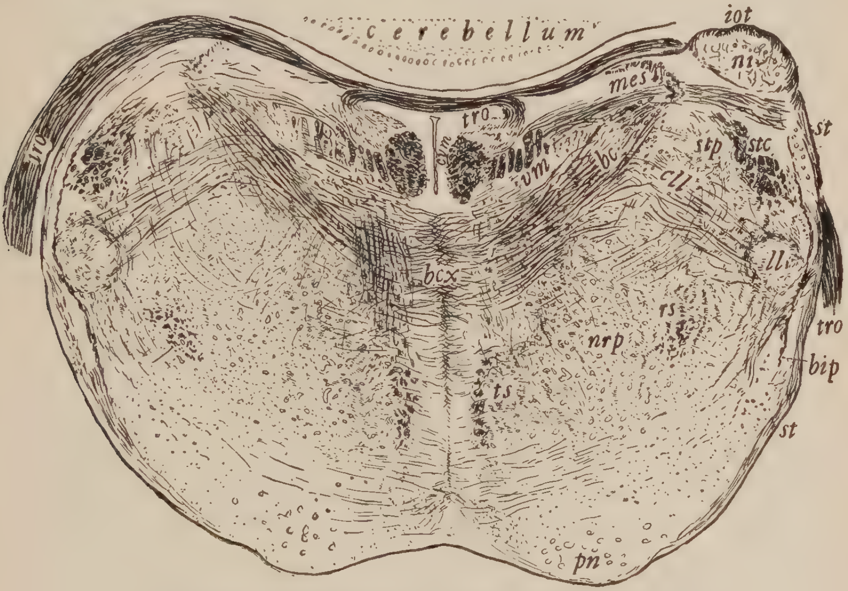

FIG. 245. Section through isthmus, of robin, × 13.

The deep cerebellar nuclei are represented by a convoluted lamella of cells often broken up into several separate masses (fig. 244, *fas*, *nd*). These receive fibers from the Purkinje cells of the cortex. The medial group of cells (*fas*) gives origin to the brachium conjunctivum (*bc*) that passes ventrally into the bulb and decussates in the isthmus (fig. 245, *bcx*). Here a large number of collaterals enter the pontal reticular nucleus (*nrp*). Above the decussation, the brachia conjunctiva (fig. 246, *bc*) pass upwards on each side of the midline to end in the red nucleus (fig. 247, *rn*).

The red nucleus is situated in the medial part of the tegmental region of the midbrain. It gives origin to a large rubrospinal tract (*rs*) of fibers which crosses the midline and descends through the reticular formation (*rt*). Their course can be readily followed medial to the lateral lemniscus and then ventral to the descending trigeminus root. In the cord (fig. 239, *rs*) they take up a typical position lateral to the dorsal horn. The brachia conjunctiva and rubrospinal tracts appear to be the chief descending tracts into the cord from the cerebellum.

The lateral cerebellar nuclei (*nd*) also give origin to a large uncinate fasciculus (*uf*) which passes ventrally to end in the vestibular nuclei. This connection between the cerebellar and vestibular nuclei is a short and intimate one. This is the other principal efferent connection of the cerebellar nuclei. Its function is no doubt concerned with vestibular tonus so important in the static and equilibritory function of Birds.

The inferior olive (*von*) in Birds is a rather well-developed structure and its fiber relations (*oc*) to the cerebellum are like those of the pontal nuclei.

The **midbrain of Birds** is complex in form and internal structure due to the great development of the **tectum** or optic lobes (figs. 246 to 249) and the nucleus isthmi in its posterior part. The cerebellum (*cb*) occupies the median dorsal region and the tectal vesicles are displaced to each side. The **optic nerves** (*ot*) are of large size. There is a complete crossing of each nerve ventral to the thalamus (figs. 249, 250, *ot*), so that the right nerve reaches the left tectum and the left nerve the right tectum. There is no superficial gray layer and the optic nerve spreads over the entire surface as a fibrous envelope (*ot*). Moreover, a large band of fibers (*gt*) from the geniculate body enter the inner surface of the tectum. Thus the tectum must be considered as having a double optic innervation. The middle gray stratum (*mgs*) consists of a number of layers of cells which form a sort of an optic cortex. This gives origin to the large tectospinal tract (*ts*) which passes through the geniculotectal tract (*gt*) and forms a fiber layer on the inner surface of the gray matter. Part of these fibers cross ventral to the cerebellum forming the tectal commissure (figs. 247, 248, *csc*). The main part of these fibers pass medially through the midbrain as long arch-like strands (figs. 246, 247, *ts*). They cross the midline between the oculomotor nerves (*om*) and descend on each side of the midline as the tectospinal tracts. A large number of these fibers enter the oculomotor nuclei (*om, tro, cil*). This system of connections is believed to mediate movements of the head, eyes and limbs in response to vision. The tectospinal tract (*ts*) constitutes a direct reflex pathway from the tectum to motor nuclei. The ventral part of the tract (fig. 246, *ts*) enters the tegmental region (fig. 247, *teg*) and is described as passing down into the bulbar region without crossing.

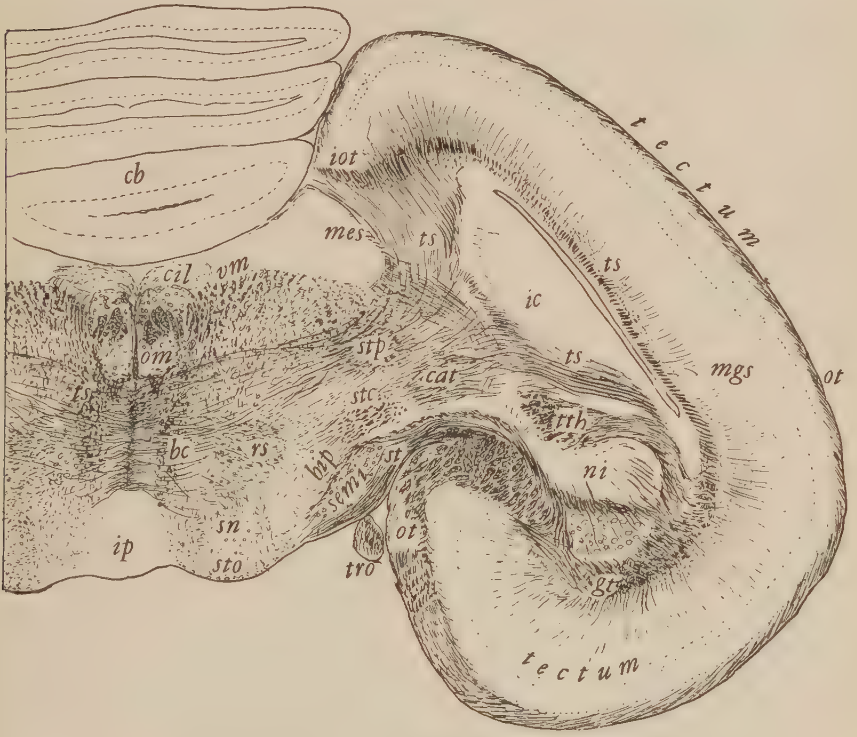

FIG. 246. Section through lower midbrain, × 12.

The **nucleus isthmi** or ganglion isthmi is a large cell mass located in the interior of the ventral and caudal part of the tectum (figs. 245–247, *ni*). In the intervening sections it curves dorsally to reach the upper border of the isthmus (fig. 245, *ni*). It consists of three closely related parts. The smaller isthmic portion forms a small elevation in the isthmus (fig. 245, *ni*). Its most important connection is the dorsal band of the optic tract known as the isthmo-optic tract (*iot*). It is described as arising in the nucleus and passing to the retina. Other connections appear as fibers on the lateral side (*st*) which connect it with the semilunar nucleus (*semi*) and with the principal part of the nucleus isthmi (*ni*).

The principal part of the nucleus isthmi (figs. 246, 247, *ni*) is a large plate of cells curved within the back part of the tectum. Its smaller outer segment consists of large cells. Several fiber connections are seen. A band of fibers (*st*) connects the nucleus isthmi with the semilunar nucleus (*semi*) and possibly with the medial geniculate nucleus (*mg*). This latter gives origin to the transverse commissure (*gc*). Another tract of coarse fibers (*bip*) comes from the large cells of the nucleus isthmi and passes down to the region of the pons, and enters the cerebellum (Craigie). A large group of fibers, the geniculo-tectal tract (fig. 247, *gt*), arises from the posterior part of the lateral geniculate body and spreads out in the posterior and ventral interior of the tectum between the nucleus isthmi and the gray matter (*mgs*) of the tectum. From the principal part (*ni*) of the nucleus there comes the large tectothalamic tract (*tth*). It occupies a more central position and passes upwards (fig. 248) to end in the nucleus rotundus (fig. 249, *tth, rot*). From the nucleus rotundus there arises a large tract of fibers that enters the thalamofrontal bundle (*tf*) medial to the nucleus and passes forward to the striatum. These connections of the tectum and nucleus isthmi through the nucleus rotundus and the thalamofrontal tract appear to form a special visual sensory system developed highly only in Birds. It is probable that it deals with spatial and object perception necessary in flying and feeding, and other sensomotor activities peculiarly developed in Birds. The relation of the nucleus isthmi to the auditory system is a close one.

The **posterior commissure** (fig. 248, *pc*) is a prominent band of fibers connecting the frontal regions of the midbrain. It takes origin from the pretectal nuclei (*npc*) seen on each side. These nuclei receive optic fibers around the frontal border of the tectum. The fibers of the commissure (*pc*) cross the midline ventral to the tectal commissure (*csc*) and curve down to end in the large interstitial (*is*) cellular masses lateral to the ciliary (*cil*) and oculomotor nuclei (*om*). This appears to be the chief optic connection to the oculomotor and ciliary centers, and can be regarded as an important reflex eye regulating mechanism. The interstitial nucleus is believed to contribute fibers into the tectospinal tracts.

The **striomesencephalic tract** (*sto*) is an important one in Birds. It can be traced from the striatum down through the thalamus into the ventral surface of the midbrain. Here its fibers (fig. 247, *sto*) stream dorsally and enter an ovoid mass of cells, the reticular nucleus of the midbrain, above the red nucleus and at a lower level a mass of cells *(sn)* comparable to the substantia nigra of Mammals. A small part of the tract enters the interstitial nucleus *(is)* above the red nucleus (fig. 248). In addition to the brachium conjunctivum *(bc)* which ends in direct relation to the red nucleus this system of fibers *(sto)* is the most obvious connection of this region ending in the socalled substantia nigra *(sn)* and reticular nuclei which appear to stand in intimate connection with the red *(rn)* and interstitial *(is)* nuclei. This tract *(sto)* appears to be the chief striatal connections of the interstitial, ciliary and oculomotor nuclei and red nuclei. It probably constitutes a striokinetic system for releasing purposive associated movements of eyes, head and limbs.

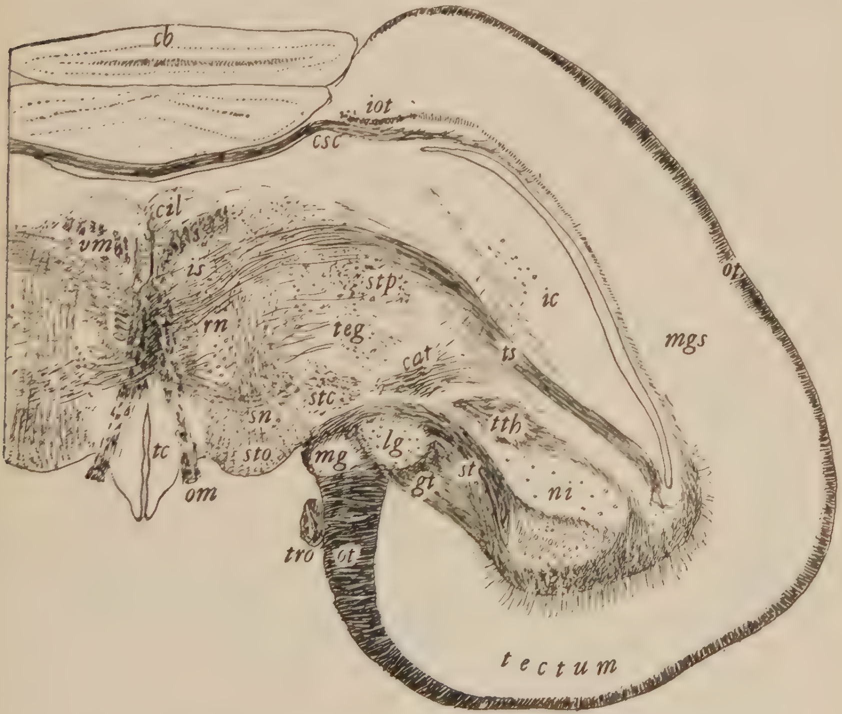

FIG. 247. Section through red nucleus, × 22.

The **lateral geniculate nucleus** is formed on the ventral side (fig. 248, 249, *lg*). On the lateral side are several biscuit-like nuclei *(lat)* in relation to the nucleus of the posterior commissure. Another nucleus *(not)* is found in the anterior margin of the tectum. These nuclei *(lg, lat, not)* receive fibers of the optic tract and send a system of fibers medially over the caudal side (fig. 248, *or*) and around the ventral side of the nucleus rotundus (fig. 249, *rot*). These fibers (*or*) join the striomesencephalic tract (*sto*) and pass upwards to the striatum. Medial to the geniculate body (*lg*) there appears another nuclear mass which gives rise to the transverse or geniculate commissure (fig. 248, *gc*) which passes through the posterior part of the optic chiasma. More forward the lateral geniculate body becomes the basal optic nucleus (figs. 249, 250, *bon*). This also receives optic fibers and radiates a large quantity of fibers dorsally into the anterior nucleus (*ant*) and the anterior lateral (*lat*) nuclei of the thalamus. In this loose spray of fibers appears the intercalate nucleus (*it*). This whole system appears to form an opticosensory connection with the striatum.

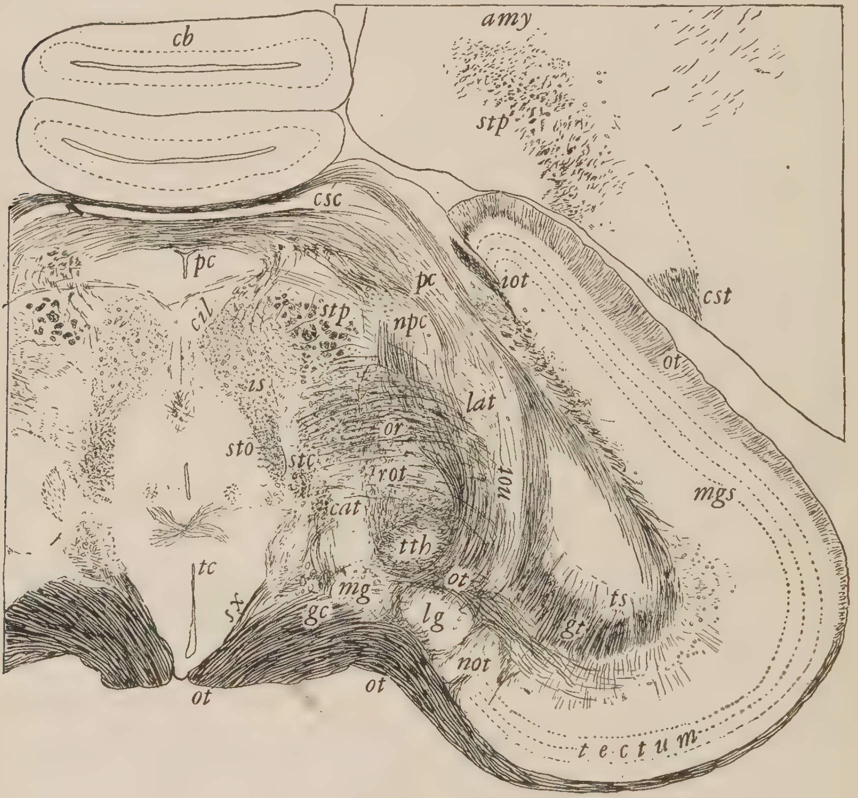

FIG. 248. Section through the posterior commissure, × 12.

The **lateral lemniscus** (*ll*) takes origin from the cochlear nuclei (*ac*, *vcn*) as two bands of fibers (fig. 242, *as*, *tb*). These cross the midline, surround the superior olive (figs. 243, 244, *so*) and pass upwards as the lateral lemniscus (fig. 245, *ll*) which surrounds a nuclear mass. From this nucleus of the lateral lemniscus fibers (*cll*) cross the midline. The lateral lemniscus extends upwards and medial to the semilunar nucleus. It enters the lateral mesencephalic nucleus (figs. 246, 247, *ic*) or torus semilunaris which forms the central gray in the interior of the tectum. From this a central acoustic tract (*cat*) passes forward between the tectothalamic tract (*tth*) and the striocerebellar tract (*stc*) and appears to send fibers into the largest part of the medial geniculate body (*mg*) between figures 248 and 249. Here, medial to the nucleus rotundus (*rot*), the tract (fig. 249, *cat*) turns dorsally to end in the spiriform nucleus (*spir*). From this nucleus (*spir*) fibers are contributed to the thalamofrontal bundle (*tf*) and pass to the striatum. This probably

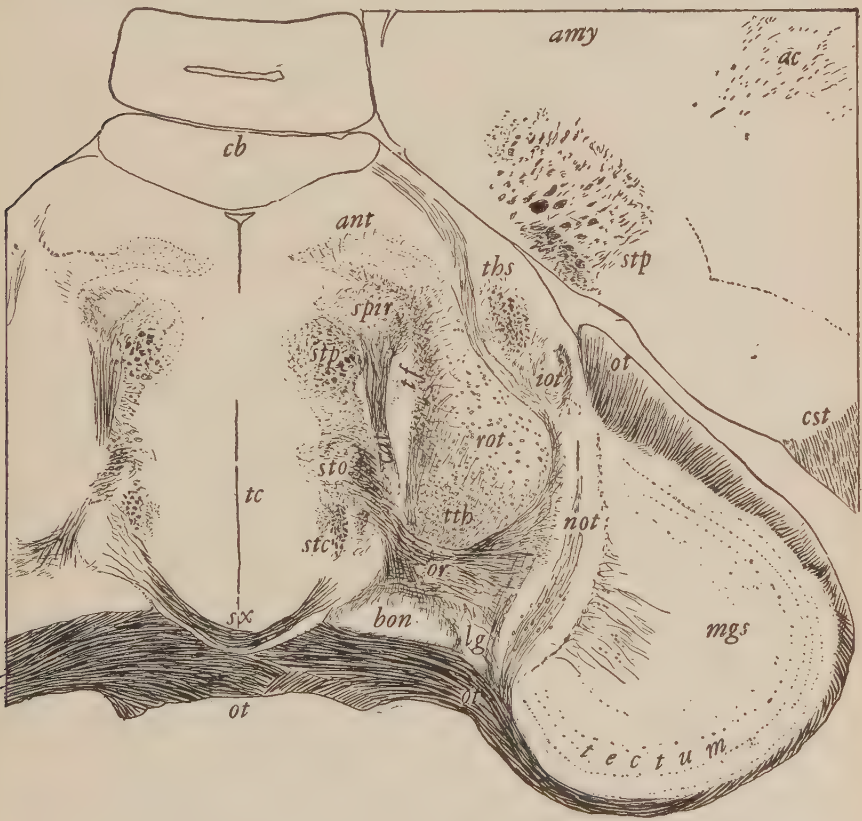

Fig. 249. Section through middle of thalamus, × 12.

forms an auditory conduction system to the forebrain. Some authors state that the lateral lemniscus also connects with the semilunar nucleus (*semi*) and nucleus isthmi (*ni*), which would put it in direct (reflex) connection with that highly developed visual mechanism.

The pontal trigeminal nucleus (fig. 244, *tn*) is connected forwards by a tract of fibers which is partly crossed (Wallenberg). The course of this ventral tract would be close to, if not identical with, the striocerebellar tract (*stc*). It is probable that fibers pass up also in the striobulbar tract (*stp*).

The nucleus cuneatus (fig. 240, *cn*) gives origin to arcuate fibers that pass across the midline. These proprioceptive tracts and spinal and bulbar sensory tracts no doubt pass upward to the tectum and thalamus. But they are so small in Birds that they cannot be followed with certainty in ordinary preparations and are not indicated in the figures.

The **thalamus of Birds** (figs. 248–250) consists of a number of dwarfed nuclear masses through which pass the large fiber bundles that connect the forebrain with the midbrain and cerebellum. The nucleus rotundus (*rot*) is the largest. It receives the tectothalamic tract (*tth*) and contributes a large quantity of fibers to the thalamofrontal tract (*tf*). Forward and dorsal to the nucleus rotundus is the anterior lateral nucleus (*lat a*). It receives a part of the large radiation (fig. 250) from the optic tract and basal optic nucleus which radiates dorsally through the thalamofrontal bundle (*tf*) into the anterior (*ant*) or dorsomedial nucleus. Both nuclei (*lat, ant*) contribute fibers to the thalamofrontal bundle. This bundle (*tf*) is formed along the medial side of these sensory nuclei (*rot, ant, lat*) and is comparable to the striatal radiations in the internal capsule of Mammals (fig. 170). The spiriform nucleus is a small mass that receives the central acoustic tract (*cat*) and contributes fibers to the thalamofrontal bundle. The posterior lateral nucleus (*lat*) and the adjacent nucleus (*not*) receive fibers from the optic tract and contribute ascending fibers (*or*) to the medial forebrain bundle (*sto*). The geniculate body (*lg*) receives optic fibers and contributes fibers (*gt*) into the deep surface of the tectum. The medial geniculate nucleus (*mg*) sends fibers to the spiriform nucleus and into the transverse commissure (*gc*).

The basal forebrain bundles are formed by three prominent tracts (*stp, sto, stc*). Due to the atrophy of the tuber (*tc*) and the medial group of thalamic nuclei in Birds these bundles have an exaggerated medial position. The **striobulbar tract** (*stp*), recently described by Craigie in the humming bird and Morgan in the cat and man, takes origin from the amygdalar region or archistriatum. These regions are connected by the amygdalar division of the anterior commissure (*ac*). From its origin it curves into the dorsal part of the thalamus and passes medial to the spiriform nucleus (*spir*) down through the lateral portion of the midbrain. Here it becomes markedly reduced at the level of the tegmental nucleus (fig. 247, *teg*). In the isthmic region (fig. 245, *stp*) its fibers pass in part to the other side. The tracts end in the masticator (*mn*) and facial (*f*) nuclei. This is probably a striomotor tract for pecking, feeding and swallowing.

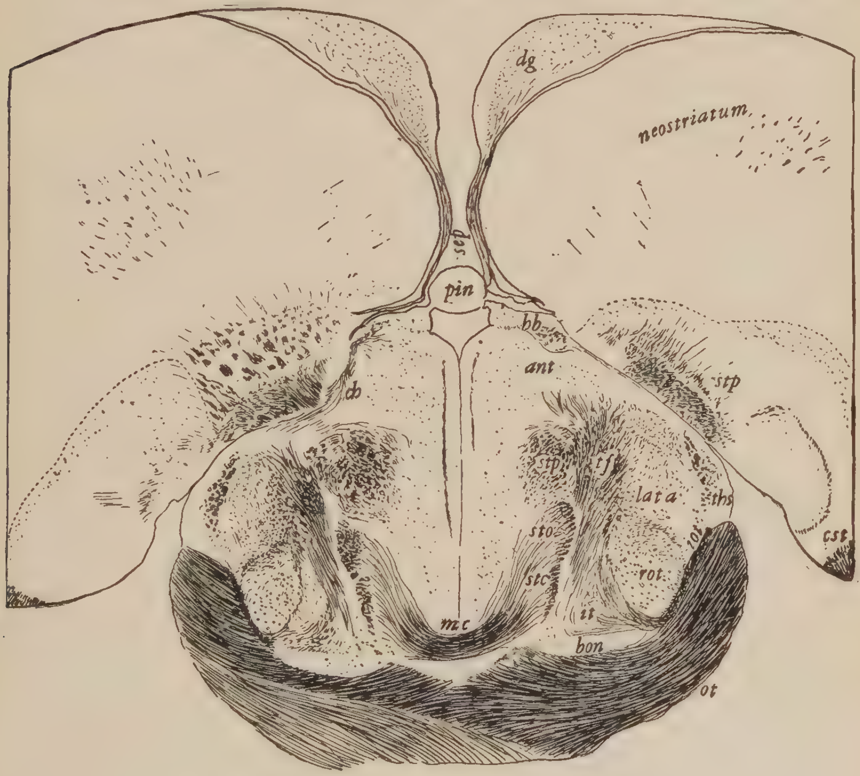

Fig. 250. Section through front of thalamus, × 10.

The **striomesencephalic tract** (*sto*) has been described (page 422) as ending on the reticular nuclei lateral to and in front of the red nucleus. In its course through the thalamus (figs. 248, 249) it receives a large accession of fibers (*or*) from the optic nuclei (*lg*, *lot*, *not*), so that above this level the bundle consists of two components. The optic fibers (*or*) are probably ascending and the striatal fibers (*sto*) are descending. At a higher level (fig. 250) the bundle (*sto*) has in relation to it a small nuclear mass which gives rise to the large supraoptic commissure of Meynert (*mc*).

The **striocerebellar tract** (*stc*) can be traced from the basal region of the forebrain (fig. 252). With other olfactory projection fibers it passes down ventral to the striomesencephalic tract (*sto*). Where it enters the thalamus (fig. 250) it connects with a small nucleus that sends fibers to the other side. It passes the thalamus, midbrain and isthmic region without interruption or diminution in size and enters the cerebellum. Its polarity is uncertain; Kappers has described it as an ascending bundle. Wallenberg's quintofrontal tract follows the course of this bundle or may be identical with it.

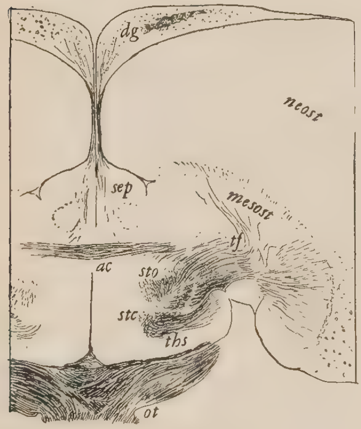

FIG. 251. Section through the region of the anterior commissure.

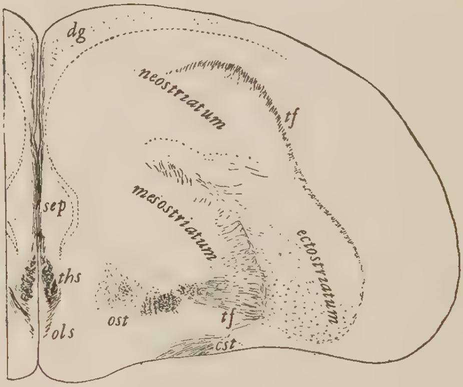

FIG. 252. Section through middle of forebrain.

The **septomesencephalic tract** is a large tract that extends down from the septal region of the forebrain (fig. 252, *ths*). Where it enters the thalamus it makes a sharp lateral turn (fig. 251) and passes down in the lateral wall of the thalamus (figs. 250, 249) to end in a nucleus in the caudal part of the thalamus in the region of the lateral nucleus (*lat*). A part of the tract enters the dorsal portion of the tectum. It is regarded as a descending and as a motor bundle from the frontal medial part of the forebrain.

The **habenular nucleus** is seen on the dorsal side of the thalamus (fig. 250, *hb*). It receives a small olfactohabenular and a corticohabenular (*ch*) tract, and sends a small habenulopeduncular bundle to the region of the tuber cinereum (*tc*). The mammillary bodies and their connecting tracts are practically absent although non-myelinated bundles may be present. This atrophy is due to the fact that in Birds the taste and smell nerves are reduced to almost extinction, least in water birds.

The **forebrain of Birds** is microsmatic to the extreme. The olfactory nerves, bulbs and all the fiber systems connected with smell are insignificant. The vomeronasal organ is absent as in crocodiles. The dorsal medial wall is formed by a rudimentary hippocampal formation (*dg*). A true cortex is not developed, but some myelinated fibers pass down into the septum. The medial wall or septum (*sep*) is reduced to a thin structure through which runs the large septomesencephalic tract (*ths*) whose origin is in the medial frontal region. A small tract of olfactoseptal fibers (*ols*) enter the septum from the ventral side as in Reptiles.

The olfactory tubercle and region of the olfactory striatum is poorly developed but gives origin to the large striocerebellar tract (*stc*) and fibers that descend to the lower level of the thalamus. The lateral ventral surface sends a frontoepistriate tract (*cst*) posteriorly into the posterior part of the striatum as in Reptiles.

The **striatum** is remarkably developed in Birds in relation to a group of sensory radiation from the thalamus (*tf*). It appears as a great thickening in the ventral and lateral wall which fills up the interior of the brain and displaces the ventricle to the dorsomedial margin of the brain. It is analagous to the somatic striatum of Mammals. It is divisible into several parts.

The posterior part that forms the caudal pole corresponds to the amygdala and is called the archistriatum (figs. 248–250, *amy*). It is connected with its fellow of the other side by a small but distinct anterior commissure. It gives origin to the striobulbar tract (*stp*) which descends through the thalamus and midbrain to end in the midbrain and in the masticator and facial nuclei. In this region ends the frontoepistriate tract (*cst*) and the corticohabenular tracts (*ch*) take their origin.

A section through the middle of the forebrain shows its subdivision into a central portion, the paleostriatum (*ost*), a middle segment, the mesostriatum and a large dorsal lateral portion, the neostriatum whose ventral fibrous part is called the ectostriatum.

The fiber tracts enter between the basal paleostriatum (fig. 251) and the mesostriatum. The striobulbar tract (*stp*) turns back into the amygdalar region. The lateral thalamofrontal tract (*tf*) coming from the nucleus rotundus, spiriform, anterior and lateral nuclei of the thalamus radiates laterally through the mesostriatum into the overlying ectostriatum and neostriatum which seem to be the chief sensory areas of the striatum. From the region of the neostriatum comes the large striomesencephalic tract (*sto*) which descends to end in the oval nucleus and substantia nigra in the region of the red nucleus. This tract has associated with it a group of ascending thalamic fibers from the optic nuclei (fig. 249, *sto*) which appear to radiate into the medial portion of the neostriatum. The striocerebellar tract (*stc*) takes origin in the paleostriatum and descends to end in the cerebellar cortex.

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CHAPTER 36

THE BRAINS OF THE AMPHIBIANS

THE young of frogs, toads and salamanders begin life as gill breathing tadpoles or larvae. In this larval stage they resemble their lower kin, the Fishes, in structure as well as mode of life. On the basis of brain structure they are closely related to the Mudfishes, including Dipnoi or lung fishes. To become adult land forms most Amphibians undergo a remarkable transformation. They develop limbs, lose their lateral line organs and their gills and develop lungs, so that locomotion, respiration and environmental receptors are profoundly altered to meet the conditions of terrestrial life. The adult salamanders in their general structural organization resemble the more primitive and unspecialized Reptiles. The frogs and toads are aberrant forms. The fact that Amphibians begin life in water as fish-like forms and finally transform into terrestrial lizard-like or frog forms is taken as evidence that the higher vertebrates, Reptiles, Birds and Mammals have evolved from ancestral stock resembling the Mudfishes and Amphibians. The Amphibia were much more abundant in the early geological era known as the Devonian, when the great inland marshes were being converted into dry land for at least a part of the summer season. The intermediate position of the Amphibians is also clearly indicated in their brain structure, which stands between that of the Mudfishes and Reptiles. It is recognized that the frogs and toads (Anura) are aberrant forms

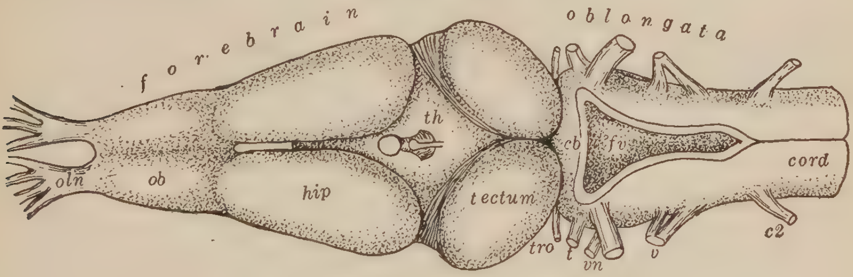

FIG. 253. The brain of a frog, dorsal view.

specialized in a direction quite divergent from that taken by the Reptiles. But the less specialized lizard-like salamanders appear to be more closely related.

The brain of the frog

Because of the general use of the frog in experimental laboratories, its brain may be studied as the most generally useful type of Amphibian nervous system (figs. 253, 254, 255). It is formed on a plan similar to that of a Urodele (figs. 261, 262), but differs from it in the greater development of several of its parts. Thus, the olfactory bulbs (*ob*) are separated from the rest of the hemispheres by a shallow constriction. The posterior parts of the hemispheres (*amy*) are enlarged and project backward concealing the thalamus (*th*). The optic lobes or tecta of the midbrain are greatly enlarged. The thalamic parts are also enlarged. In these respects the brain of the frog begins to resemble the brain of a primitive Reptile. The hindbrain or oblongata is chiefly a terminal center for the cranial nerves. The cerebellum (*cb*) is of small size but larger than that in the sluggish Urodeles. This is a condition which also prevails in the Reptiles though to a lesser extent.

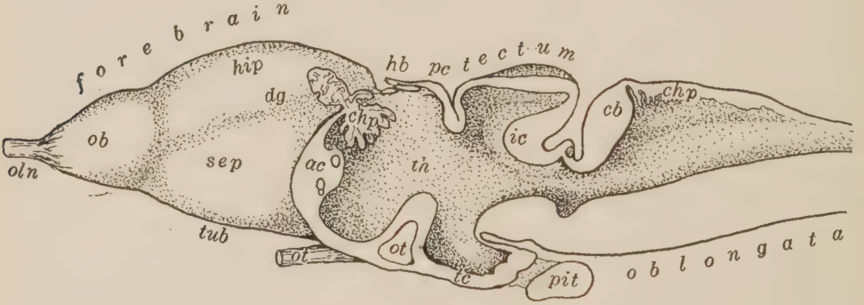

Fig. 254. Median surface of right half of the brain of a frog. After Osborn.

The **spinal cord** is connected with each of the ten pairs of spinal nerves by means of a small ventral and a larger dorsal root. The spinal ganglia are found in the sensory dorsal roots to which their cells give origin. Cervical and lumbar enlargements occur in the cord in relation with the large nerve roots of the nerves that supply the upper and lower limbs. The lower end of the cord is reduced to a slender cone, to which an additional coccygeal nerve may be attached.

A cross section of the cord shows a typical *H* form of the **gray matter** around a central canal. The dorsal horns, though still small, are clearly separated from each other. The ventral horns contain the still simply arranged groups of motor cells which give origin to the ventral roots. The collaterals that enter the gray matter from the dorsal columns of root fibers, the intermediate nucleus and the ventral commissure are other evident structural features. The **white matter** is formed of (about 60,000) longitudinal fibers. The dorsal columns between the dorsal roots over the dorsal horns are formed by the sensory fibers of the dorsal roots which arise in the spinal ganglia. By means of collaterals they make connection with the dorsal and ventral horn cells and nucleus intermedius. Where the cord joins the oblongata the dorsal columns are large, due to the fact that the trigeminus (*t*), and the vestibular (*vn*) nerves send down long descending roots in these columns. Indefinite nuclei cuneatus and gracilis such as occur in Reptiles and Mammals have been recognized in the frog, and also internal arcuate fibers passing ventrally from them. The lateral and ventral white columns of the cord are formed chiefly of **fasciculi proprii** which arise from the small cells of the intermediate nucleus and end by means of collaterals in the ventral horn at different levels of the cord. The **ventral commissure** is the crossed fasciculus proprius. These fasciculi mediate the coördinated spinal limb reflexes. On the lateral surface there are two ascending tracts, the **spino-cerebellar** (fig. 257, *dsc*) that enters the cerebellum, and the **spino-tectal** (*st*) that enters the tectum and ends in the anterior tegmental nucleus of the midbrain. Besides the roots of the cranial nerves that pass down in the dorsal columns there are two large tracts that pass down in the

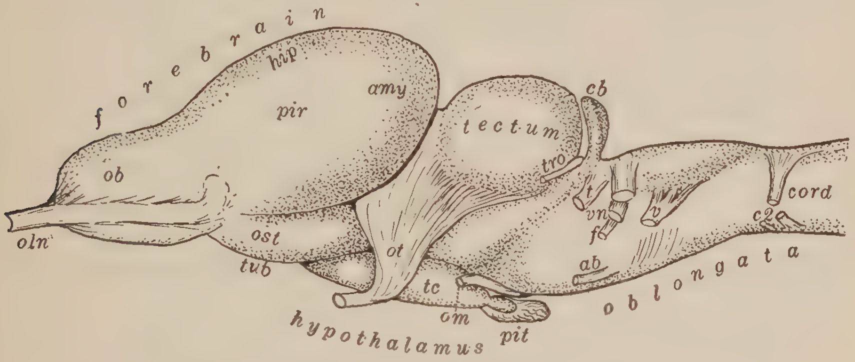

Fig. 255. The brain of a frog, left side. After Gaupp.

ventral columns of the cord. The **tectospinal** (*ts*) from the tectum is the chief motor tract; it mediates visual reflex responses. The **vestibulo-spinal tract** (*vs*) from the vestibular nuclei is the chief supraspinal tract for tonic and equilibritory responses.

The **oblongata** (fig. 253) is primitive and its resemblance to that of Petromyzon (fig. 298) is noticeable. It consists of two out turned lateral walls whose dorsal borders are widely separated but are roofed over by a membranous roof (*chp*) containing a vascular plexus. There is no perforation in this roof for the escape of fluid. The enclosed space is the fourth ventricle (*fv*). In front it is bordered by the cerebellum which does not overhang as in the turtles (fig. 218). Ventral to the cerebellum it is continued into the ventricle of the midbrain and thalamus. The lateral walls of the oblongata (fig. 255) provide the central connections for the 5th to the 11th cranial nerves. There is recognized a lateral sensory area entered by the sensory nerves and a medial motor area containing the motor nuclei and the large motor fiber bundles which end on them. In the walls of the oblongata the columnar arrangement in connection with the nerve roots and fiber bundles is by no means as accentuated as in the Fishes, but more nearly approaches the conditions in Petromyzonts.

The **cranial nerves** connected with the oblongata (fig. 256) have a rather primitive arrangement. The first cervical nerve has been observed in the embryo but is suppressed in the adult or what there remains of it is fused with the second cervical (*c 2*). The **hypoglossal nerve** (*hy*) is likewise still a part of the 2nd cervical in its most anterior ventral root. This is a primitivism since in higher vertebrates the nerve separates from the cervical nerves and with its nucleus shifts to a more forward position. The **spinal accessory nerve** forms the most caudal motor rootlet of the vagus (*v*). The vagus (*v*) in its anterior rootlet also includes the **glosso-pharyngeal nerve** of higher forms. This fusion of the glosso-pharyngeus and spinal accessory with the vagus may be considered as a primitivism or an actual reduction in the frog. These nerves are attached to the lateral side of the oblongata between the vestibular and *c 2* and along the descending root of the trigeminus. To the inside of the latter the sensory filaments of the vagus group turn down and form the **solitary fasciculus** (*sf*) in the characteristic vertebrate position. The columns of cells associated with the solitary fasciculus are as in other terrestrial vertebrates rather reduced, due no doubt to the loss of the gills and reduction of the taste buds.

The **vestibular nerve** (*vn*) which innervates the cristae of the canals, saccule and utricle has a ventral and a dorsal root. The ventral root is in the position usual in other higher forms. It ends as a descending root that forms an elevation (*dvn*) along the dorsolateral border of the oblongata. Along the inner surface of this root extends the descending vestibular nucleus which gives origin to vestibular arcuate fibers that cross in the midline. At the point of entrance of the nerve are the large cells that form the lateral vestibular nucleus which contributes vestibulo-spinal fibers (fig. 257, *vs*) into the reticular formation. Similar fibers extend upwards in the medial longitudinal fasciculus (*vm*) to the trochlear and oculomotor nuclei (*om*). It seems that these vestibular centers and tracts are a mechanism for the performance of the tonic postural reactions that have been demonstrated (Maxwell) to result from stimulation of the vestibular organ. These vestibular centers are also connected to the cerebellum by a fiber system probably comparable to the uncinate fasciculus of higher forms (fig. 150, *uf*). The spinocerebellar tracts (*dsc*) of the frog also pass to the cerebellum. The cerebellum, though small in the Amphibians, on the basis of its fiber connections may be regarded as a special cellular field which stands in intimate relations to the vestibular mechanism and its tonic and dynamic functions.

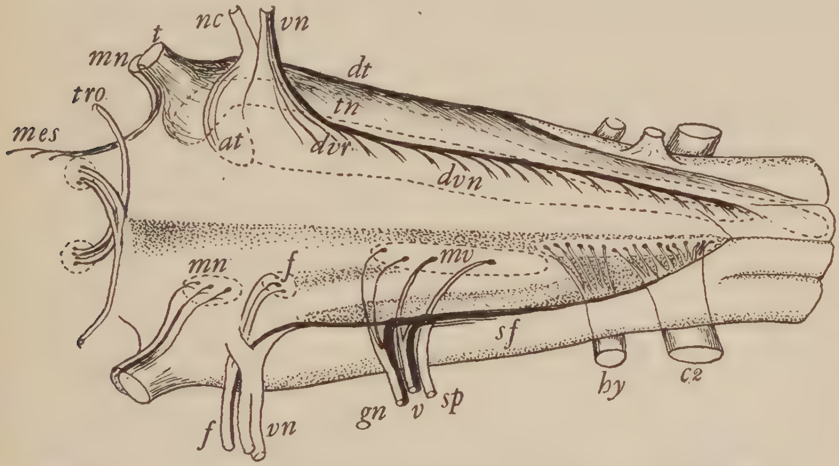

FIG. 256. Plan of cranial nerve roots of a frog. Dorsal view of oblongata.

The dorsal root of the vestibular nerve (*nc*) supplies the crista of the posterior canal and also the papilla of the lagena and the papilla basilaris. Since these latter primordia of the cochlea occur here for the first time (Retzius) the dorsal root forms in part the primitive cochlear nerve. It ends in the dorsal border of the oblongata near the base of the cerebellum in the dorsal acoustic nucleus (fig. 256, *at*). From this region a bundle of fibers (*ll*) passes around the outer side of the oblongata to end in the posterior thickened part (*ic*) of the tectum. This system is therefore the forerunner of the cochlear centers, lateral lemniscus and inferior colliculus of higher forms. It is connected forward by the geniculate commissure (*gc*).

The **lateral line nerves** are present in the Urodeles and in the tadpoles of Anura but are suppressed in the fullgrown frog. Vestiges of them often occur in the cochlear, facial and trigeminus nerves.

The **facial nerve** (*f*) comes from a nucleus of cells that has a dorsal position near that of the masticator (*mn*). The typical curve which the nerve makes to its exit in higher forms is quite absent. The sensory component of the facial nerve joins the solitary fasciculus of the vagus.

The **abducens nerve** (*ab*) comes from a nucleus of cells located more caudally than in higher forms. The **trochlear** (*tro*) comes from a nucleus near the midline and crosses through the roof plate that joins the cerebellum with the tectum. The larger **oculomotor nerve** (*om*) comes from a nucleus near the midline ventral to the tectum. It makes a direct ventral exit. These three nerves supply the eye muscles. Their nuclei of origin (fig. 256) are placed near the midline, lined up along the course of the vestibulo-mesencephalic tracts (*vm*) and the tectospinal tracts (*ts*) that form the medial longitudinal bundle.

The **trigeminus nerve** (*t*) springs from the trigeminal ganglion (prootic). Its root enters the oblongata in front of the vestibular and passes down on the surface through the vagus roots into the spinal cord. All along its course it ends on a long descending nucleus which joins the dorsal horn of the cord. A typical pontal nucleus is wanting. The mesencephalic root springs from large ganglion cells in the posterior part of the tectum and joins the masticator nerve or motor fifth to supply sensory endings in the muscles. The **masticator nerve** (*mn*) springs from a motor nucleus close to that of the facial, passes out with the trigeminus root and distributes to the mandibular muscles.

The **midbrain** is conspicuous on account of the large optic lobes or **tectum** on the dorsal side. These are large hollow vesicles containing an extension of the ventricular cavity. This condition resembles that seen in some bony Fishes, Reptiles, and embryos of Mammals. In the frog the eye has become the chief extroceptive sense organ and the size of the tectum is due to the increase in the central connections of the optic tracts. The **optic tract** (*ot*) is likewise large. It crosses with its fellow, forming the chiasma ventral to the hypothalamus (*tc*), then it embraces the thalamus and midbrain to reach the whole antrolateral margin of the tectum, through which it is distributed as the optic stratum. The tectum also receives the **spinotectal tract** (*st*) which enters the anterior part and ends also in the dorsal thalamic nucleus (*dor*). The cellular cortex of the tectum is the fusion center for these sensibilities. It gives rise to the large **tectospinal tract** (*ts*) which curves around the ventricles to cross the midline and descend near the oculomotor nuclei (*om*), along the midline down to the cord. This is the main reflex tract from the tectum and doubtless mediates the important optic reflexes of the frog.

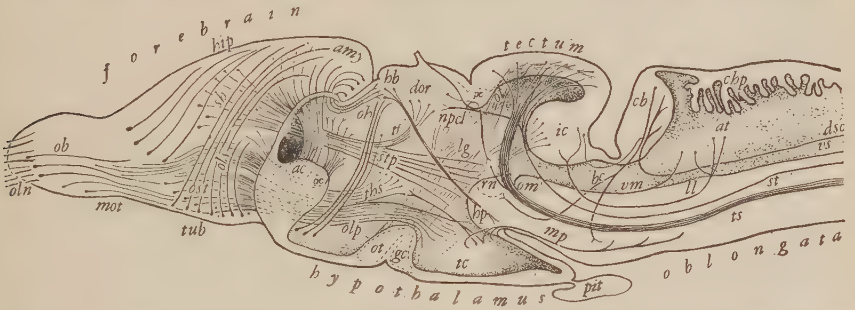

FIG. 257. Plan of fiber tracts of the brain of a frog, projected on the median surface.

As the optic tract embraces the thalamus, cellular masses are included in its course (fig. 257). These are the lateral geniculate body (*lg*), the pretectal nucleus (*npc*) and the dorsal thalamic nucleus (*dor*). The latter is rather long and the habenular nuclei appear in front of it. It is from this cellular region that the fibers of the posterior commissure (*pc*) arise. They pass through the commissure to end in the region of the nucleus reticularis magnocellularis (*rn*) in front of the oculomotor nucleus. From this, fibers enter the tectospinal tracts. From the dorsal thalamic nucleus a small fasciculus of fibers (*tf*) is also described as passing forward in the lateral forebrain bundle to the forebrain cortex. A comparison with the mammalian thalamus (fig. 166) will show how these nuclear connections of the optic tracts of the frog resemble those of the nucleus of the optic tract (*not*), nucleus of the posterior commissure (*npc*) and dorsal nucleus of the thalamus (*dor*). The other sensory nuclei are wanting in the frog. The lateral geniculate (*lg*) is to be compared only with the ventral (*striatal*) and often insignificant part of the lateral geniculate body of Mammals. The striocortical connection that the lateral geniculate (*lg*) makes in the Reptiles (fig. 236) is not developed in the frog.

The **inferior colliculus** (*ic*) is seen as a thickening in the posterior wall of the tectum as in Reptiles. It receives a fiber tract, the lateral lemniscus (*ll*), that passes around the oblongata from the acoustic tubercle (*at*). A band of fibers, the **geniculate commissure** (*gc*), from the lateral region of the tectum joins the optic tracts and crosses behind the chiasma to the same region of the other side as in Reptiles and Mammals. These structures in the frog are the forerunners of the higher auditory connections.

The **dorsal thalamus** (*dor*) is closely related to the optic centers. The habenular body (*hb*), however, has the connections typical of other vertebrates. A corticohabenular tract (*ch*) enters it through the lateral wall and an olfactohabenular tract (*oh*) enters it through the medial wall of the thalamus. The **habenulo-peduncular tract** (*hp*) connects the habenula with the interpeduncular nucleus (*ip*). This appears to be an efferent or motor system from the caudal parts of the forebrain.

The **hypothalamus** consisting largely of the tuber cinereum (*tc*) receives from a more caudal region the tract known as the mammillary peduncle (*mp*), and in addition, according to Kappers, a tertiary gustatory tract from the ganglion isthmi lateral to the inferior colliculus. The hypothalamus is more extensively connected forward with the forebrain by means of the forebrain bundles as in Fishes and Reptiles. These connections with the olfactory forebrain are believed to constitute feeding and other neural mechanisms dealing with metabolic functions.

The **forebrain** of Amphibia consists of two evaginated hemispheres connected at the front end with the olfactory nerves. In the salamanders the olfactory bulbs still appear as an integral part of the hemispheres but in the frog they are marked off by shallow constrictions and the bulbs are secondarily fused with each other. The cavities or lateral ventricles (*lv*) communicate with the third ventricle around a narrow interventricular foramen (*for*) which still marks the region around which the forebrain evagination took place in a lateral direction. In front of the foramen the hemispheres are united by a terminal plate, the ventral part of which is thick and occupied by the anterior commissures (*ac*) while the dorsal part (or lamina supraneuroparica) is still thin and forms a median dorsal sac. In front of the terminal plate a median sagittal fissure separates the hemispheres (fig. 253) except where the olfactory bulbs (*ob*) are secondarily fused in the frog. Paleontological evidence shows that the ancestors of Amphibia were primitive Ganoids closely related to the Dipnoian stock with which their forebrains are to be compared.

The **walls of the forebrain of Amphibia** are thin and laterally compressed. Though more advanced in differentiation they closely resemble those of Mudfishes (Ganoids and Dipnoi). The **medial wall** is formed by two characteristic parts (fig. 254). The septum (*sep*) and the primordium hippocampi (*dg*, *hip*). The lateral wall (fig. 255) consists of an anterior part (*pir*) and of the posterior part or lateral olfactory region (*amy*) connected with the anterior border of the thalamus back of the interventricular foramen. The narrow ventral wall is formed by the olfactory region (*tub*) more closely related to the septum. The dorsal and medial wall consists of a hippocampal formation (*hip*) still in a primitive stage of development. The rudiment of the cerebrum seen in Reptiles (fig. 219, *cer*) is wanting in Amphibia, in general, although a vestige of it is thought to occur in the adult frog. The hind part of the lateral wall (*amy*) that forms the posterior pole of the forebrain and joins the thalamus is said to receive some afferent fibers (fig. 257, *tf*) from the dorsal nucleus of the thalamus (*dor*) through the lateral fore-

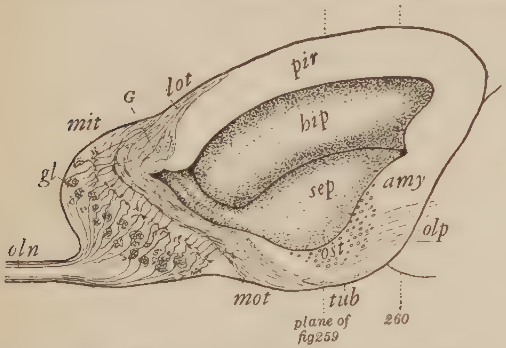

FIG. 258. Forebrain of frog, left side. The lateral wall has been removed to show the ventricular eminences formed by the primordium hippocampi (*hip*) and the septum (*sep*).

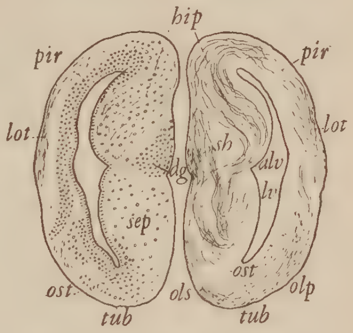

FIG. 259. Cross section through the middle of the forebrain of a frog. The plane of the section is indicated in figure 258.

brain bundle (*stp*). This region corresponds to the epistriatum of the Selachians (Johnston) and amygdala of Reptiles and may be an area for the fusion of olfactory impulses with other sensibilities brought in by the thalamic fibers (*tf*). From the front all the walls of the forebrain are reached by secondary olfactory fibers from the olfactory bulb, and the forebrain of Amphibia as that of Fishes may be considered as mainly an organ for the reception and intensification of impulses of olfactory origin and for their transmission through the forebrain bundles into the lower motor systems.

The **olfactory bulbs** (*ob*) arise in a dorso-lateral position but soon shift to the front. In the frog (fig. 255) a considerable length of the olfactory nerve is still attached along the side so that for some distance a lateral (so-called " accessory ") bulb is present. This is not the same accessory structure that is found on the medial side in Reptiles and Mammals. The structure of the olfactory bulb of the frog is shown in figure 258. The lateral position of the olfactory nerve and bulb is seen. The three characteristic structures are: first, the entering olfactory nerve fibers (*oln*), second, the zone of glomerule (*gl*) or ball-like synapses formed between the olfactory nerve fibers and the dendrites of the mitral cells, and third, the mitral cells (*mit*) specialized pyramidal elements whose dendrites enter the glomeruli and whose axones run back through the granular layer (*G*) into the brain wall and form the olfactory tracts (*lot*).

The end of the forebrain into which the olfactory bulb is implanted is called the anterior olfactory nucleus. In higher forms it becomes converted into the olfactory peduncle and a proximal part known as the trigone. Through these the olfactory tracts that arise from the mitral cells of the bulb pass back to the more highly developed centers in the lateral, ventral and medial walls of the forebrain.

The **lateral olfactory tract** in the frog takes an extreme dorsal course in the forebrain wall (fig. 259, *lot*). The more ventral position of these tracts in the Reptiles (figs. 216, 232) is due to the formation of a more extensive piriform and hippocampal cortex both of which are still in a rudimentary state in the frog. The dorsal lateral wall in relation to the lateral olfactory tract may be considered as the piriform area (figs. 258, 259, *pir*). Some fibers from the ventral striatal region appear also to enter this area.

The **medial wall** is divided into two characteristic parts, the hippocampal primordium (*hip*) and the septum (*sep*) separated by sulci seen on both the medial and the ventricular surfaces. As seen in figures 258 and 259 these parts form prominent bulgings into the ventricle. The **hippocampal rudiment** (*hip*) receives olfactory fibers (*ols*) from the anterior olfactory nucleus which spread out in the surface layer, and on a more caudal level fibers (*sh*) also enter a more restricted area which forms the supracommissural nucleus (fig. 259, *dg*). This whole dorsal medial surface and the nucleus may be regarded as a receptive area comparable to the dentate gyrus of higher forms. The hippocampus (*hip*) forms the dorsal ventricular bulging which in the dorsal wall unites with the piriform area (*pir*). There is no clear separation between the receptive area (*dg*), the hippocampus (*hip*) and the piriform area (*pir*). The cells in the

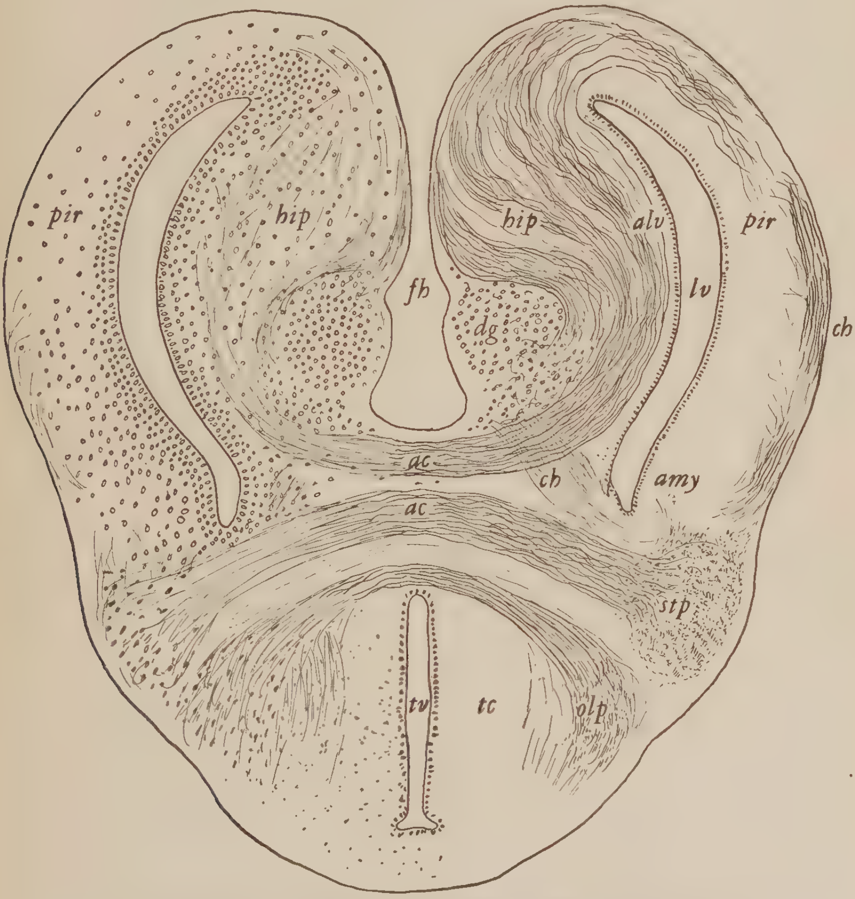

FIG. 260. Cross section through the region of the anterior commissures of a frog. Plane of section is indicated in figure 258.

hippocampal region are more scattered and give rise to a tract of fibers in the alveus (*alv*) near the ventricular surface. Some of them curve medially through the narrow region of the sulcus to enter the medial forebrain bundle (*olp*). It is probable that they form a primitive fornix (P. Cajal). The majority pass back to enter the dorsal division of the anterior (pallial) commissure (*ac*). This commissure is in part equivalent to the septal or fornix commissure (*fxc*) of Reptiles and Mammals and probably in part to the commissure of the terminal stria.

The **septum** (*sep*) forms the ventral bulging in the medial wall. It is an extension of the anterior olfactory nucleus and as such receives olfactory fibers, a large tract of which passes back to enter the ventral division of the anterior commissure (*ac*). A large tract of olfacto-septal fibers (*ols*) passes dorsally to enter the region of the dentate gyrus (*dg*); a connection with the thalamus through the medial forebrain bundle (*ths*) is also present.

The **ventral wall** in its anterior part is formed by the olfactory tubercle (*tub*) which receives diffuse olfactory fibers from the bulb. Its deeper portion adjoining the ventricle (*lv*) is specialized into a striatal nucleus (*ost*) which extends around the medial border into the septum as the nucleus (*accubens*) septi as in Reptiles and Mammals. A large diffuse tract of fibers called the forebrain bundle (*olp*) extends down to the hypothalamus. In its medial border this bundle probably includes thalamoseptal fibers and the primitive fornix. As the bundle (*olp*) enters the hypothalamus it forms the most ventral component of the anterior commissure (fig. 260) and then according to P. Cajal divides into two components. The medial one crosses and both components end in the wall of the tuber (*tc*).

The lateral forebrain bundle becomes a distinct structure in the caudal portion of the forebrain (fig. 260, *stp*). This region may be for convenience designated as the amygdala (*amy*) since it corresponds to the lateral olfactory nucleus and amygdala of Reptiles and Mammals. A large bundle of thalamic fibers (*tf*) enters the surface of this region in relation to which an area of cells is differentiated in the wall of the brain. The deeper part of the brain wall is here also specialized as a striatal nucleus (*amy*) and gives origin to the lateral forebrain bundle (*stp*) which descends into the ventral part of the thalamus. It also gives origin to the large middle division of the anterior commissure (*ac*).

The brain of Amblystoma

The brain of the Urodele Amblystoma (figs. 261, 262) may be taken as an example of the primitive Amphibians related to Mudfishes. The brain as a whole is small and simple in form and shows little of the crowding and bending seen in higher vertebrates. In internal structure also, it is generalized and may be taken as a prototype of the higher forms. A slight predominance of development is shown by the forebrain in connection with the olfactory nerves, the tectum connected with the optic tracts and the oblongata connected with the lower cranial nerves. The olfactory bulbs and hypothalamus are large. The thalamus proper though small shows a certain degree of development proportional to that of the forebrain with which its development is associated. The cerebellum (*cb*) is rudimentary as in most inactive forms.

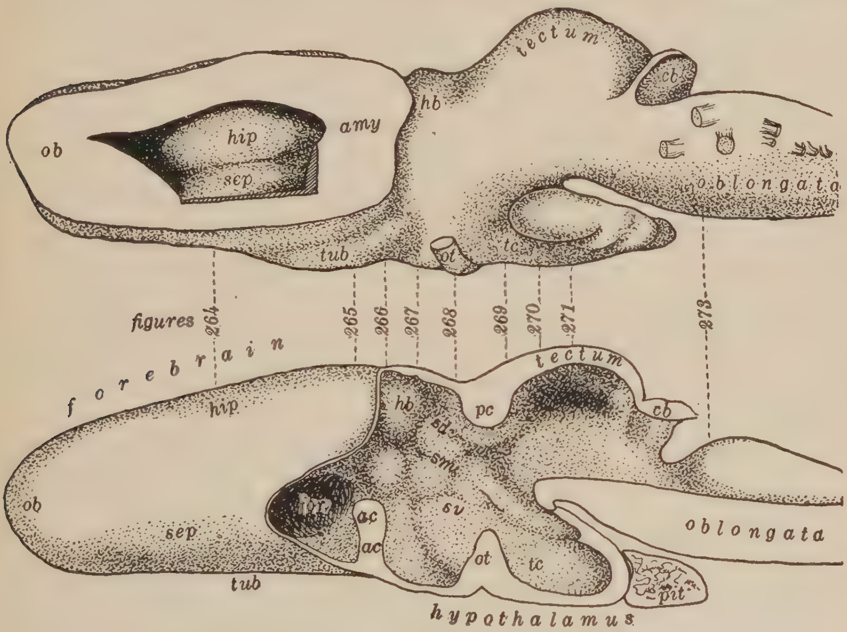

FIG. 261. Lateral side of brain of Amblystoma, × 10.
FIG. 262. Medial view of brain of Amblystoma, × 10. From C. J. Herrick.

The **forebrain** is evaginated laterally and forward in the form of two tubular vesicles containing an extension of the ventricular cavity. The olfactory nerve fibers terminate in the front end of the vesicles chiefly in its lateral side. The olfactory bulb which is thus formed extends far back on the lateral surface.

Beyond this the lateral wall extends back as the lateral olfactory region or primitive amygdala which curves medially to join the unevaginated thalamus. Here a groove is formed on the outer side which forms the natural line of demarkation between the two. On the inner surface this is formed by the posterior border of the interventricular foramen (fig. 262, *for*). The union of the lateral wall with the thalamus is always thick and structurally important.

The medial wall of the forebrain vesicle is thin at its front end, but farther back it becomes thickened in its dorsal and ventral parts (*hip sep*). In figure 261 the lateral wall has been removed to expose these bulgings of the hippocampus (*hip*) and septum (*sep*). A comparison of this with the condition in the frog (fig. 258), the turtle (fig. 218) and a Monotreme (fig. 50) reveals a fundamental similarity. The septum (*sep*) is joined with the ventral wall of the brain which shows a thickening of the olfactory tubercle (*tub*). The hippocampus is related chiefly to the dorsal lateral wall but extends backward into the upper end of the amygdalar region (*amy*). A thin terminal lamina connects the medial wall of the two sides. In the posterior ventral part is a large transverse ridge formed by the anterior commissure (*ac*) which unites the amygdalar regions of the forebrain vesicles. Neither a true septal (*fxc*) or posterior pallial commissure (*hc*) are developed in Amblystoma.

In the minute structure of the Amblystoma, Professor Herrick has demonstrated a remarkable wealth of detail which makes possible an extensive comparison of its primitive nervous system with the brains of other vertebrates. Throughout, it shows a primitive stage of differentiation, very instructive in the light which it throws on the morphogenetic history of the nervous system of higher vertebrates.

The structure of the front end of the forebrain is that of an olfactory bulb (fig. 263). The fibers of the olfactory nerve (*oln*) form an outer fiber layer (*F*) and end in a layer of glomeruli (*gl*). Small periglomerular cells (1) connect the glomeruli. The large mitral cells (*mit*) send their dendrites to arborize in the glomeruli and their axones (*a*) pass caudally in the lateral and ventral olfactory tracts. Smaller less differentiated cells (*g*) form a thick internal granular layer. The less differentiated cellular area where the bulb joins the septal and lateral walls is called the anterior olfactory nucleus (*ant olf nuc*).

The structure of the forebrain is shown in figures 264 and 265. The cells occupy a primitive central position around the ventricle.

They show a high degree of proliferation so that special cellular areas or "nuclei" can be recognized. Only in the hippocampal region (*p hip*) have cells migrated to the surface forming a primitive cortex. Elsewhere only their dendrites branch towards the surface and come into relation with fibers from the olfactory bulb and from the thalamus.

The connections of the hippocampal, septal and dorsolateral regions are chiefly olfactory. The primordium hippocampi (*p hip*) is a well-differentiated cellular area. A less differentiated dorsal area (*p p d*) is seen united by fibers with the hippocampal area. The septum is differentiated into a medial (*nuc m s*) and lateral nucleus (*nuc l s*). An olfactoseptal tract (*tr ols*) passes from the ventral region through the medial wall of the septum into the medial margin of the hippocampus. Fibers in the ventricular surface of the hippocampus converge posteriorly to form the ventral hippocampal commissure (*com hip*). Ventrally passing fibers are also described which form the primitive fornix. The fibers coming from the olfactory bulb form the lateral olfactory tract (*tr ol dl*) which ends in relation to a cellular area (*nuc ol dl*) connected chiefly with the dorsal area (*p p d*) and hippocampus. Here also

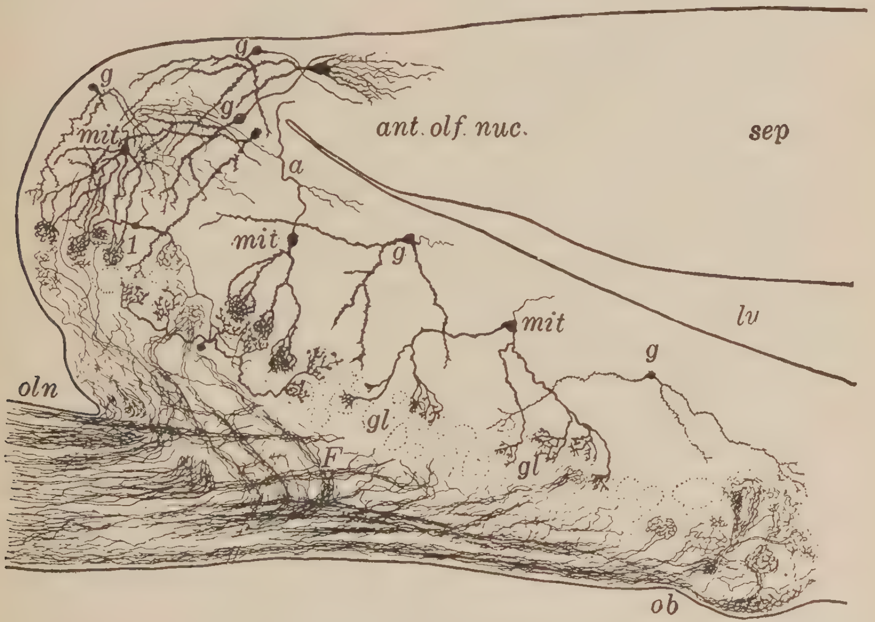

FIG. 263. Left olfactory bulb of Amblystoma, × 50. From C. J. Herrick.

arises a corticohabenular tract (*trc hab l*) which passes back over the posterior margin of the forebrain to enter the habenula (fig. 266).

The ventral area receives fibers from the olfactory bulb. Its surface is differentiated into an olfactory tubercle (*tub*) connected also with the medial forebrain bundle (*f m t*) and the olfactopeduncular tract (*tr ol ped*). The deeper cellular portion (*nuc caud*) is heavily proliferated forming a primitive olfactory striatum.

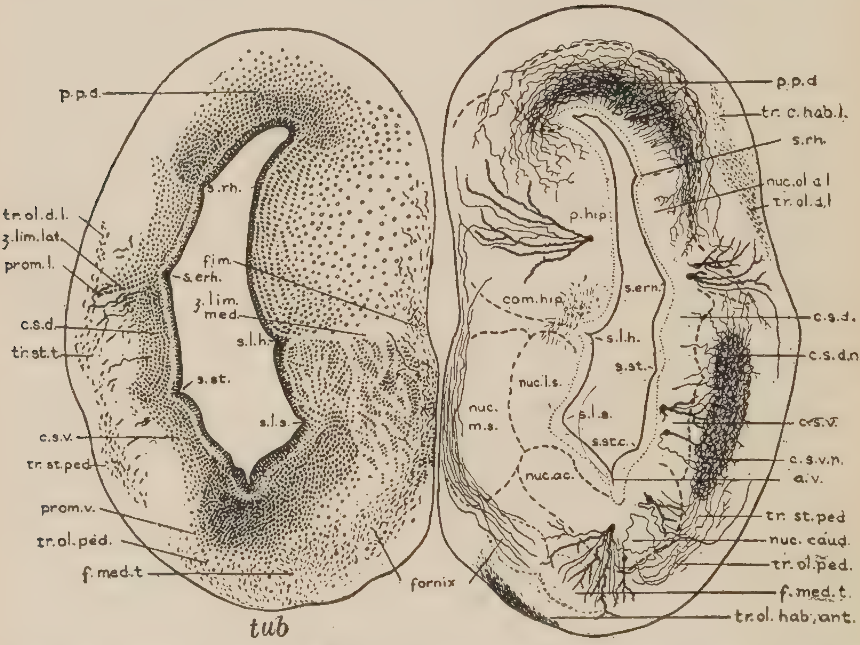

FIG. 264. Section through middle of forebrain of Amblystoma, × 28. Cells and fibers shown on left; on right some details from Golgi preparations. From C. J. Herrick. Jour. Comp. Neur. **43**. The plane of figures 264 to 273 is indicated between figures 261–262.

The ventrolateral wall has important fiber connections with the thalamus and midbrain. A sharply differentiated striatal area on the side (*csv csd*) gives origin to two important tracts, a striotegmental (*tr st t*) and a striopeduncular tract (*tr st ped*). This area is the primitive somatic striatum.

The large hypothalamic and peduncular connections can best be seen in figures 265 and 266. The medial forebrain bundle (*f med t*) in part decussates and is ending in two divisions in relation to the cells of the preoptic nucleus (*nuc po*). The lateral part forms the olfactopeduncular tract (*tr ol ped*). Together these bundles descend to end in the hypothalamic region down to its caudal limits. Olfactohabenular tracts (*tr ol hab*) and corticohabenular tracts (*tr c hab*) connect the preoptic and lateral cortical regions with the habenula.

The decussations of the several tracts of the lateral forebrain bundles through the anterior commissure is also seen (fig. 265). These occur between the posterior, striatal or amygdalar regions of the forebrain. The amygdala receives an olfactory bundle besides thalamic fibers. A large commissure (*com amg*) connects the two amygdalar nuclei. The primitive ventral position of the hippocampal commissure (*com hip*) is noteworthy. Its fibers may also enter the crossed medial forebrain bundle (*f med t*). The striotegmental tract (*tr st t*) comes from the striatum (*c s d n*). It forms the largest component of the lateral forebrain bundle. In the thalamus it turns dorsally to enter the dorsal tegmental region of the midbrain and some of its fibers can be followed as far down as the trigeminus. This tract is to be compared with the stripeduncular and striobulbar tracts (*stp*) of higher forms. The striopedun-

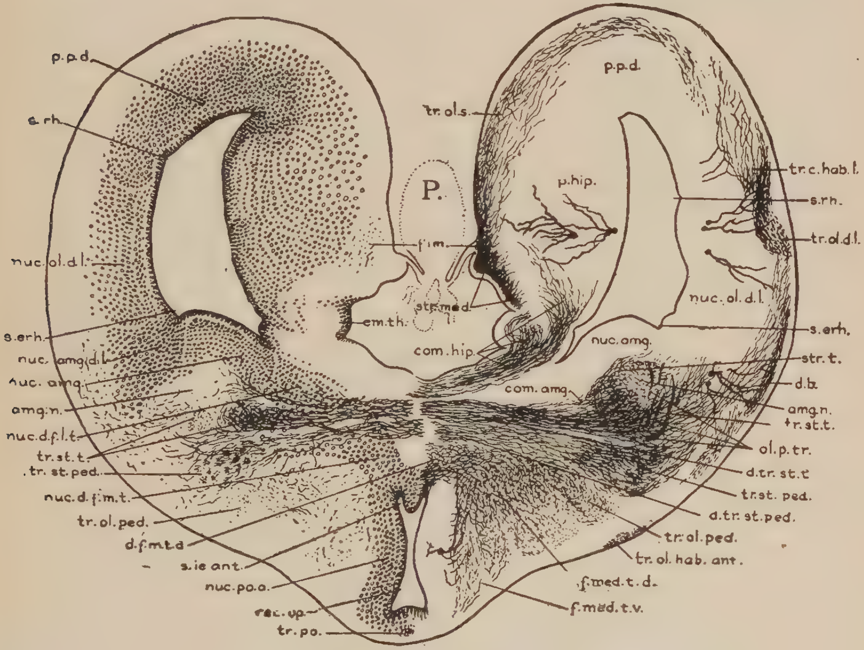

FIG. 265. Section through anterior commissure of Amblystoma, × 27. From C. J. Herrick.

cular tract (*tr st ped*) comes from the ventral striatum (*c s v n*), extends down through the thalamus to end in the tegmental region lateral to the oculomotor nerves and interpeduncular nucleus. This tract is to be compared to the striomesencephalic tract of higher forms. The thalamofrontal tract (*tr th f*) arises from cells in the dorsal thalamus and passing up with the foregoing tracts ends in the striatal region. It is comparable to the thalamic fasciculus (*tf*) of higher forms. The olfactopeduncular tract (*tr ol ped*) arises from the head of the caudate (*nuc caud*) and from the ventral striatal nucleus and descends in the ventral part of the cerebral peduncle. It is comparable to the olfactory peduncle (*olp*) of Mammals and the striocerebellar tract (*stc*) of Birds. In Amphibians, as in Fishes and Mammals in whom taste and smell are well developed, hypothalamic and preoptic connections with the forebrain are well developed.

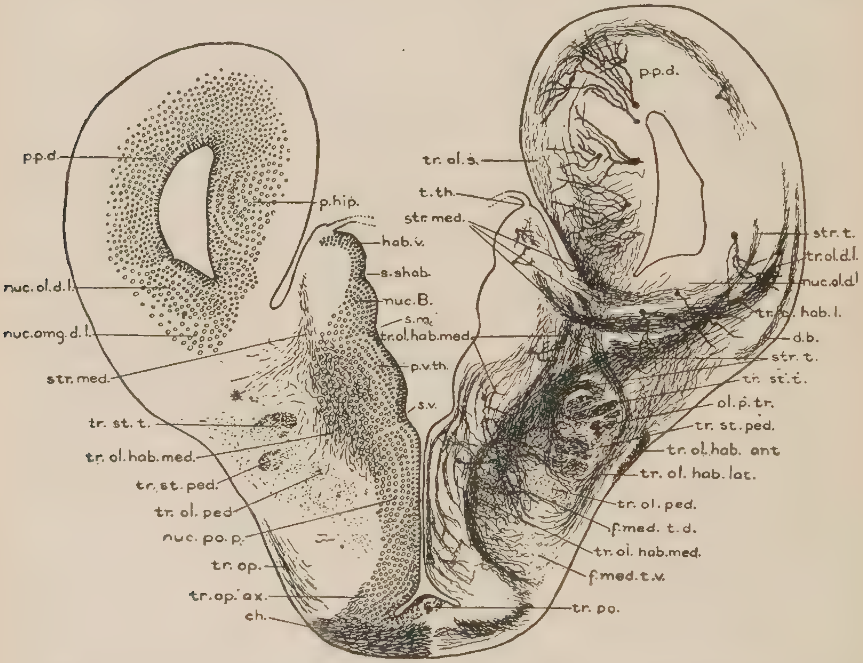

FIG. 266. Section through the optic chiasma, habenular nucleus and posterior end of forebrain, × 27. From C. J. Herrick.

The **thalamus** is limited in front by a line drawn from the front of the habenula to the preoptic region. This coincides on the outer surface with the groove that marks the posterior limits of the forebrain. From the midbrain it may be marked off by a line that joins the posterior commissure (*pc*) with the front of the posterior tubercle. It is in general a tubular structure transversely compressed. Its outer surface is covered by a stratum of optic tract fibers. Its ventricular surface (fig. 262) is modeled by a dorsal (*sd*), a middle (*sm*) and a ventral (*sv*) sulcus. These sulci separate elevations which correspond to the tracts and nuclear masses differentiated in its walls; compare figure 262 with 268.

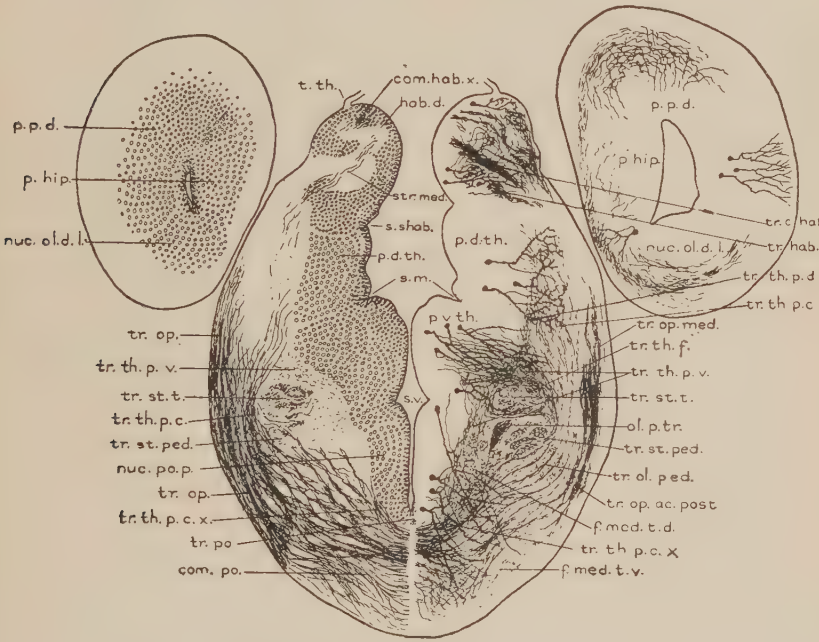

FIG. 267. Section through the anterior part of the thalamus, × 28. C. J. Herrick.

Its structure is shown in figures 266 to 269. The cells occupy the primitive periventricular position and show a number of proliferation areas. The dendrites of the cells arborize into the outer fibrous layer where they come into functional relation with various tracts which invade this layer. The dense areas of neuropile thus formed are to be regarded as synaptic areas. As yet the centrally located cells have not migrated into these synaptic areas.

In the dorsal border are the habenular nuclei (*hab*) in which terminate the medullary stria (*str med*) whose origin is shown in figure 266. From the habenular nuclei the habenulopeduncular tract (*hab ped*) passes ventrally to the interpeduncular region.

The optic tracts (*tr op*) cross on the ventral side (*ch*) and their anterior divisions end in relation to diffuse groups of cells which form the primitive pretectal and geniculate nuclei. The posterior commissure (*post com*) connects the pretectal region with the oculomotor region (*n com post*). An anterior, a posterior and a peduncular root of the optic tract are recognized which pass beyond the thalamus and end in the midbrain. A postoptic commissure (*com po*) occurs which corresponds to the transverse or geniculate commissure of higher vertebrates.

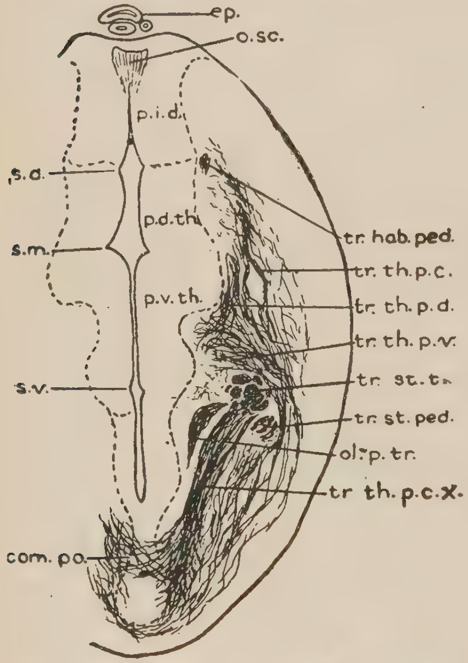

FIG. 268. Section through the middle of the thalamus of Amblystoma, × 30. From C. J. Herrick. Compare position of sulci (*sd sm sv*) with those in figure 262.

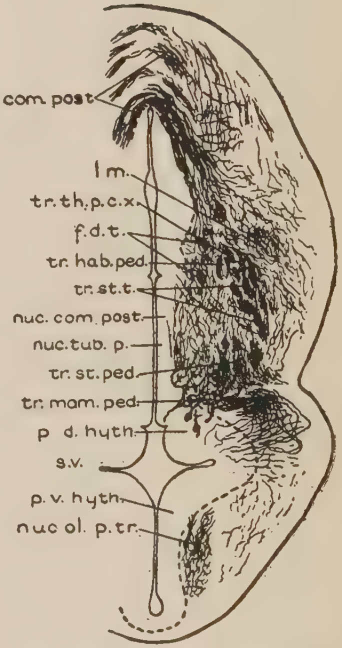

FIG. 269. Section through region of posterior commissure, × 30. From C. J. Herrick.

In the ventral lateral side are seen the large descending striotegmental (*st t*), striopeduncular (*st ped*) and olfactopeduncular (*ol p*) tracts. Sensory fibers (*lm*) reach the thalamus from caudal levels. A large group of thalamopeduncular fibers are contributed from the dorsal thalamic region (*pd th*). A considerable number of the fibers from the ventral part (*pv th*) pass to the other side through the postoptic commissure (*com po*). This region (ventral thalamus) corresponds in its general features to the subthalamus of higher forms.

The hypothalamus (*hy th*) is seen in sections back of the optic decussations (figs. 269 to 271) projecting ventrally to the subthalamus. A dorsal and a ventral part are recognized separated by the ventral sulcus (*sv*). The mammillary peduncle (*mam ped*) enters the dorsal part. The olfactopeduncular tract and fibers from the preoptic region enter the ventral part (*nuc ol p*).

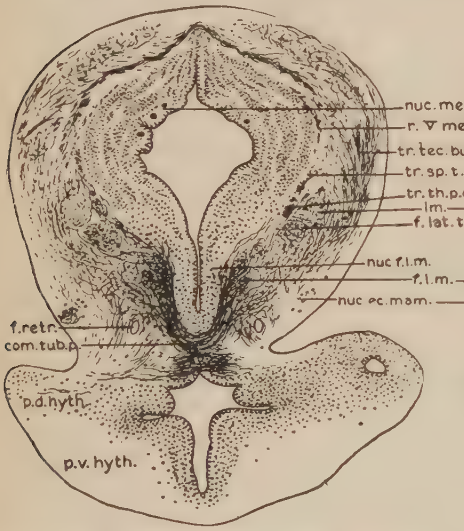

FIG. 270. Section through front of midbrain of Amblystoma.

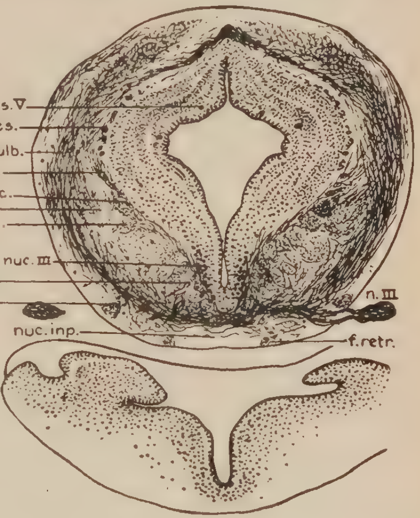

FIG. 271. Section through level of oculomotor nuclei. From C. J. Herrick. Jour. Comp. Neur. **39**.

The **midbrain** extends from the posterior commissure (*pc*) to the cerebellum (*cb*). It is characterized by the expansion of its dorsolateral wall into the optic vesicles or tecta and the thickening of its lateral walls to form the peduncles. These features give it a round contour in cross sections. The oculomotor (*om*) and trochlear (*tro*) nerves take their origin from cells within the midbrain.

Sections of the midbrain (figs. 270, 271) cut also the caudal projection of the hypothalamus ventral to it. Cellular layers surround the aqueduct. This shows a slight lateral outpouching into the tecta. The mesencephalic root of the trigeminus (*r v mes*) surrounds the cellular layers and takes its origin from large cells in the gray matter. Optic tract enters the surface of the tectum and bulbar tracts (*tec bulb*) enter its deeper layers. Tectospinal tracts (*sp t*) are also recognized. The peduncular root of the optic tract ends in relation to the ectomammillary nucleus (*nuc ec mam*). The medial longitudinal fasciculus (*f l m*) ends in relation to the oculomotor nuclei (*nuc III*). Just in front of this is the large interstitial nucleus (*nuc f l m*) which gives origin to descending fibers in the medial longitudinal fasciculus. It is also called the nucleus of the posterior commissure since the commissure makes connections with it. The descending striotegmental tract (*f lat t*) and ascending sensory tracts (*lm*) are seen passing through the peduncular region. The habenulopeduncular tract (*f ret*) ends in the side of the interpeduncular nucleus (*nuc inp*). To the side of this the oculomotor nerve (*n III*) makes its exit.

The **oblongata** of Amblystoma (fig. 272) in its form and functional connections is similar to that of other vertebrates. In most respects it may be compared to the early stages in the development of the mammalian bulb. The weak development of the cerebellum accentuates this embryonic appearance. The central canal of the cord expands into a broad *T*-shaped fourth ventricle. The lateral walls are splayed out and are united by a membranous roof containing a choroid plexus, cut away in the figure. At the caudal end the walls unite in a tubular manner as in the spinal cord. At the cephalic end the dorsal borders form the cerebellum (*c cb*) transversely placed back of the tectum (*nuc p t*); so that a sharp bend occurs between the cerebellum and acoustic area (*a ac*).

The walls of the oblongata present a weakly expressed columnar arrangement. The acoustic area forms the dorsal border of the oblongata and serves as an area of termination for the vestibular and lateral line nerves. Medial to it is a weakly developed visceral lobe (*lob vis*) in relation to which the central connections of the vagal complex of nerves are effected. In the medial and ventral region are located the motor nuclei. The positions of the ambiguus nucleus (*nuc amb*), of the abducens (*nuc VI*), of the motor facial (*nuc VII m*) and of the masticator (*nuc V m*) are indicated on the floor of the ventricle (fig. 272). A large subcerebellar eminence occurs in front of the masticator nucleus which has crowded this nucleus laterally.

The general position of the superficial nerve roots is indicated on the side of figures 272 and 273 by Roman numbers. The components of the cranial nerves can be studied out in figure 274. In the larvae of Amphibians there is a tenth and a seventh lateral line nerve (*r VII ll*) as in Fishes. The root of the trigeminus makes a slight elevation on the lateral surface. The central connections of the cranial nerves are similar to those seen in the frog (fig. 256). The acoustic and lateral line nerves end in the acoustic area by long bifurcated roots. The visceral sensory nerves descend and form the solitary bundle ending in relation to the visceral lobe (*lob vis*). The trigeminus has a short pontal root ending in relation to a large sensory nucleus in that region, and a long descending root passing down as far as the lower end of the bulb.

In the **structure of the bulb** (fig. 273) three features should be noted; the central position of the cells, the outer position of the sensory roots and fiber tracts, and the synaptic areas of neuropile which represent functional connections between the fibers and cells. The sensory nerve roots, indicated by Roman numerals, retain their individuality and position in the outer fiber layer. By means of collaterals they enter into synaptic relations with dendrites of the centrally located cells. These synaptic areas are represented by columns of neuropile for the most part devoid of cells. The black dots are cells of uncertain nature located in the fibrous areas. The scattered distribution of these early migrant cells is noteworthy. Two large special Mauthner's cells occur in the acoustic area. The motor nuclei are clusters of cells differentiated in the outer border of the cellular layer. The noteworthy bundles are arcuate fibers that cross and enter some of the longitudinal bundles. The medial

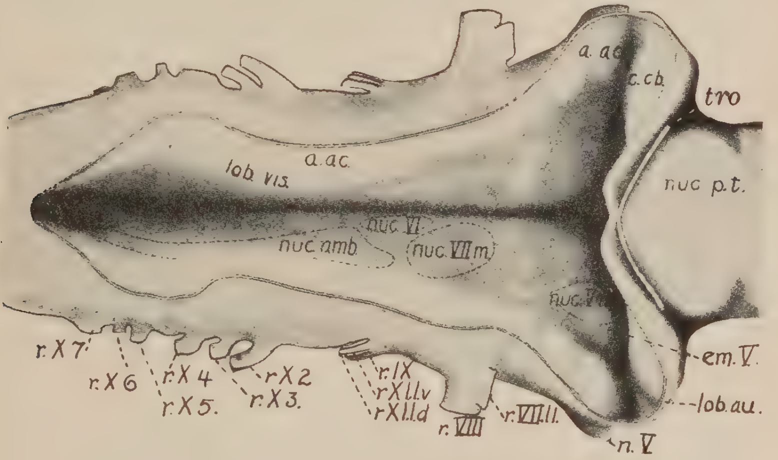

FIG. 272. Wax model of oblongata of Amblystoma, dorsal view, × 42. From C. J. Herrick. Jour. Comp. Neur. **24**.

longitudinal fasciculus (*f l m*) and the tectobulbar tracts (*tr tb*) are seen near the midline. More laterally are the medial lemniscus (*l m*), the bulbotectal tract (*tr b t*) and spinotectal tracts (*tr sp t*). Two large tracts connect the acoustic area with the cerebellum (*tr a*, *tr b*), reminding one of the restiform body and uncinate fasciculus of higher forms.

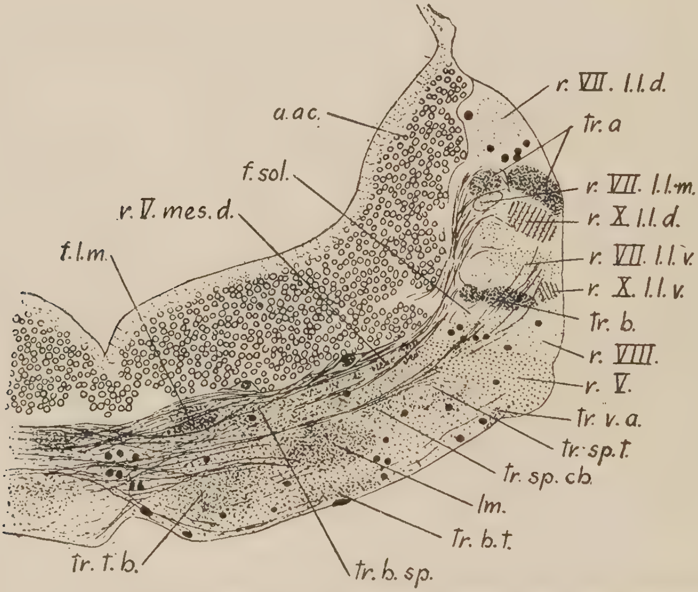

Fig. 273. Section of the oblongata of Amblystoma between facial and trigeminal roots. From C. J. Herrick.

The **cerebellum** (*c cb*) is small and is an evident continuation of the acousticolateral area, from which it receives the ascending terminals of the acousticolateral nerves. In addition two large bundles connect it with the entire length of the acoustic area (*tr a*, *tr b*, of Kingsbury). The cerebellum is a bilateral structure whose two lateral masses are connected across the middorsal plane by the cerebellar commissure. In front of this is the decussation of the trochlear nerve (*tro*) and the mesencephalic root of the trigeminus. The cells of the cerebellum, like those of the other parts of the brain, are arranged in layers bordering the ventricular surface. They appear like greatly simplified Purkinje cells. The granule cells of more highly developed cerebella have not been identified. Ventral to the cerebellum in the floor of the ventricle is the ventral cerebellar eminence whose connections are in the direction of the nuclei of the oculomotor nerves.

The **spinal cord** is a simple tubular structure connected with segmental nerves. The cell bodies retain their primitive position in the central gray and the fiber tracts and synapses form the outer fiber stratum. A dorsal sensory and a ventral motor zone are recognized. Large neurones in the ventral zone give origin to the ventral roots. The remainder of the cells are correlation neurones. The larvae are swimming forms. From the work of Coghill there appears to be very little functional localization in the cord segments of larvae. Longitudinal distribution of fibers over generalized cellular areas prevails. The earliest reflexes to appear are total crossed reactions such as swimming movements. They involve ascending afferent impulses in the dorsal tracts, decussations in the ventral commissure at upper levels of the cord and in the oblongata, and descending impulses in the ventrolateral fiber tracts of the other side. Shorter segmental mechanisms for local reflexes appear to be developed in adult Amblystoma, especially in segments that innervate the limbs.

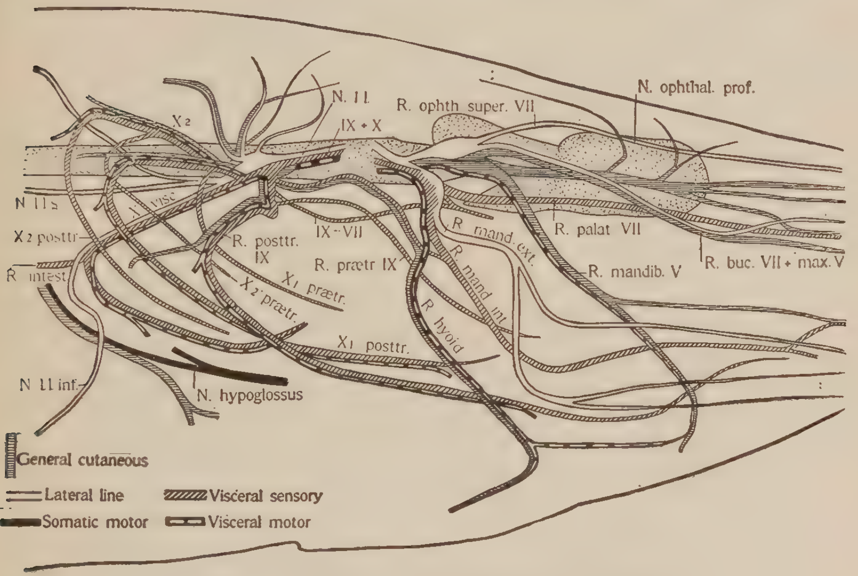

FIG. 274. Cranial nerve components of Amblystoma After Coghill from J. B. Johnston.

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CHAPTER 37

The Brains of Fishes

All Fishes are adapted to an aquatic mode of life which is reflected in the structure of their body and brain. The aquatic habitat has preserved in them a primitive mode of reproduction, respiration, locomotion, sensory receptivity and methods of securing food. The aquatic medium has always imposed on its inhabitants rigid conditions which have changed very little from the earliest geological times. In this medium the entire organization of the nervous system of Fishes has been perfected on a reflex plane, each reflex system dealing with some important reaction to this environment. Special olfactory and taste organs for testing sapid substances in water and special acoustic and lateral line organs have been perfected in the Fishes. The indications are that Fishes have been derived from an ancestral stock now long extinct, resembling the Lampreys. Certain transitory stages are represented by the primitive Lampreys, the Sharks, Ganoids and Mudfishes, though all are specialized and aberrant forms.

From early Silurian times the cartilagenous Sharks (or Elasmobranchs) have inhabited the salt waters, while the Bony Fishes (or Teleosts) have dominated fresh waters and now compete with the Sharks for the mastery of the ocean. Mudfishes possessing lungs (Dipnoi) and their allies, the primitive Ganoids, were restricted to shallow muddy and, in certain seasons, poorly aerated waters abounding with vegetable life, which has resulted in the greater development of their olfactory forebrain but less active motor systems. The brains of Sharks and Bony Fishes, though more primitive in respect to the forebrain, have developed highly differentiated reflex systems in connection with the olfactory, optic, gustatory and acousticolateral organs. The active Sharks and Teleosts have a cerebellum almost as highly developed as Birds. The forms that inhabit shallow waters may have a small cerebellum or the gustatory centers may be greatly enlarged. The more active Teleosts who depend more on vision have greatly developed optic lobes (tecta) like Amphibians, Reptiles and Birds. There is also wide divergence in body form, especially in bottom feeding Fishes such as rays, flounders, catfishes, etc. In spite of the great variation in its form in different genera, the nervous system of Fishes presents certain

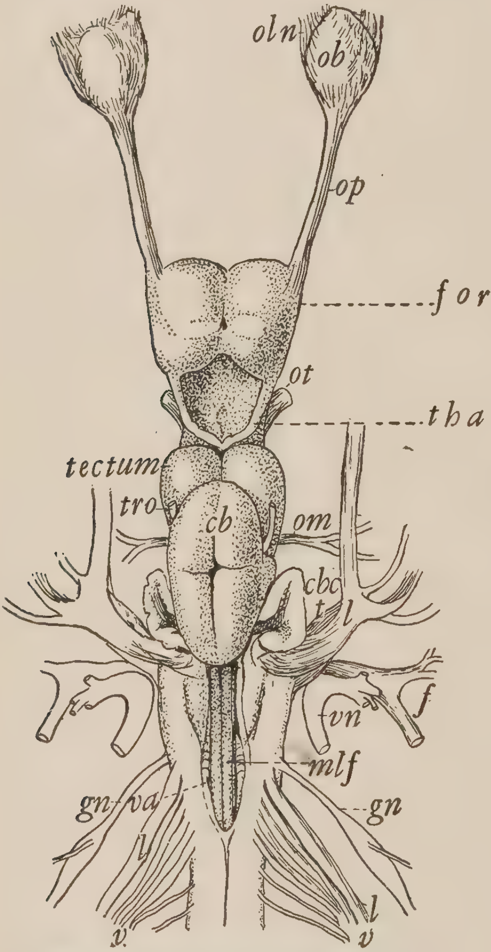

Fig. 275. Brain and nerve roots of a spiny dogfish, *squalus acanthias*, dorsal side, × 1½.

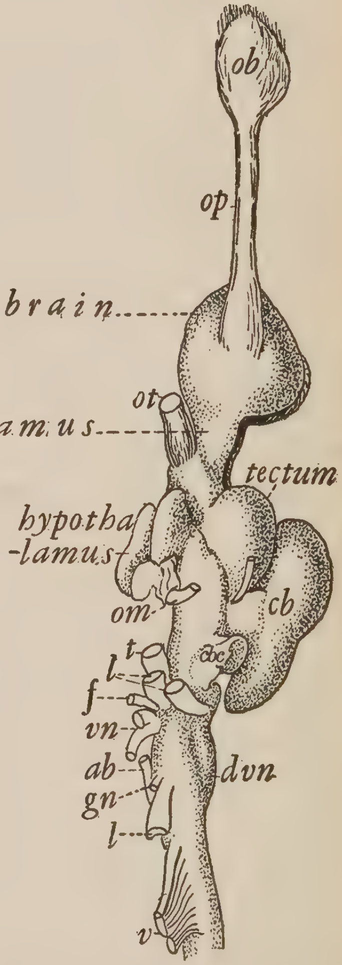

Fig. 276. The same seen from the left side, × 1½.

features common to all, as can be seen by a comparison of a Shark (fig. 275) with a Teleost (fig. 286).

The **brain of Elasmobranchs** (Sharks and Rays) only partially fills the cranial cavity, and the cartilagenous cranium can be readily cut away to expose the whole organ and the connecting cranial nerves (figs. 275–278). The brain is elongated, narrow and divisible into easily recognizable parts. The entire brain is a hollow tubular structure as in all true vertebrates. Its walls enclose a central cavity which forms the ventricles in different parts of the brain. The walls of the tube contain the nerve centers and tracts and are developed as thickenings in connection with various nerves and sense organs. It can be clearly seen that the form of the brain and its subdivisions are due to physiological connections which it makes through its nerves with various sense organs.

The forebrain is connected forward with the olfactory bulbs (*ob*).

The thalamus is a narrow segment connecting the forebrain with the midbrain, and having on its ventral side a saccular projection, the hypothalamus.

The midbrain has prominent dorsal expansions, the tecta, connected with the optic tracts (*ot*). The midbrain gives origin to the oculomotor nerves (*om*, *tro*).

The cerebellum is a dorsal, median structure with a cortex or outer cellular surface, connected with the narrow isthmic segment which unites the midbrain with the oblongata.

The medulla oblongata is an elongated segment which owes its large size mainly to the cutaneous sensory (trigeminus and lateral line) nerves and the respiratory nerves (vagus and glossopharyngeal) which are connected with it, and highly developed in Fishes.

The spinal cord is a caudal continuation of the oblongata and is connected with a long series of spinal nerves.

The **oblongata** is an elongated segment which owes its development to the central connections of the fifth to the tenth cranial nerves. A comparison of the oblongata of the dog fishes (figs. 275 to 278) with that of the sturgeon (fig. 279), a ganoid fish, or a Teleost (figs. 286, 287) shows that in each class the nerves are connected with the thickened lateral walls which enclose a large space, the fourth ventricle (*fv*). The medullary velum which roofs over the ventricle has been removed. Long ridges or columns are seen in the inner walls. They owe their existence to the difference in the peripheral distribution and function of the nerve fibers that end in them. These columns have, therefore, a functional significance derived from the peculiar distribution of the corresponding nerve components.

By the work of Gaskell, Strong, Kingsbury, Johnston, Herrick, Norris and others, it has been shown that the peripheral nerves as well as the oblongata are divided into functional divisions. This conception has been substantiated by the demonstration of nerve components in the cranial nerves and their endings in corresponding functional columns in the oblongata. The nerve components of a salamander are shown in figure 274, of a bony fish in figure 288,

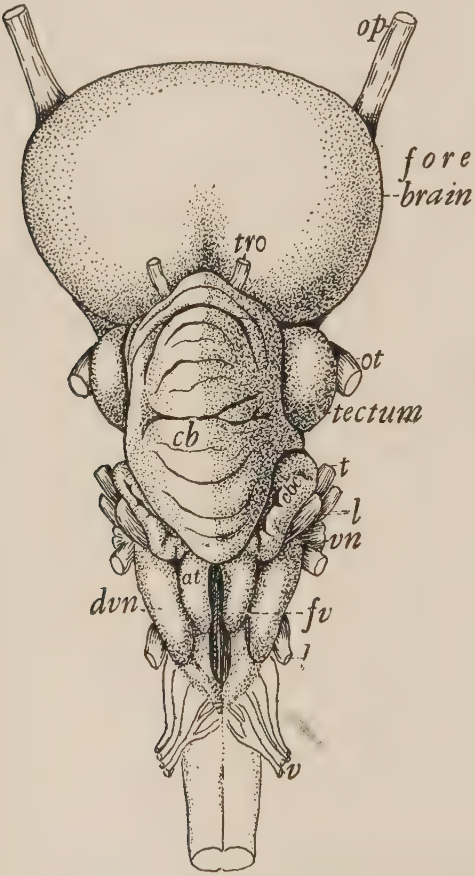

FIG. 277. Brain and nerve roots of a smooth dogfish, *mustelus canis*, dorsal side, × 1½.

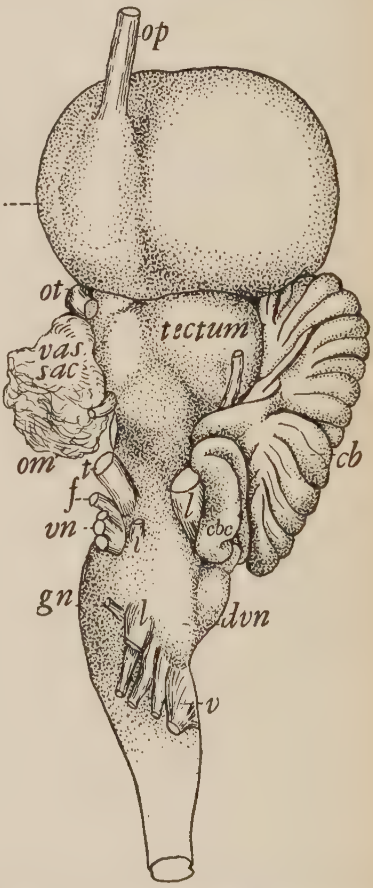

FIG. 278. The same seen from the left side, × 1½.

and of a lamprey in figure 299. In each figure the functional components in each nerve are indicated by different markings.

The **somatic sensory components** are the nerve fibers that supply the sense organs in the body wall and skin and their derivatives, the lateral line organs and the vestibule. They are indicated by parallel or horizontal lines in the figures. In function they are proprioceptive and extroceptive.

The **visceral sensory components** are the nerve fibers that supply the taste buds and sense organs or free endings in the viscera. They form the sensory facial, glossopharyngeal and vagus nerves. They are indicated by oblique lines in the figures. In function they are enteroceptive and gustatory.

The **visceral motor components** are the motor nerve fibers that supply the glands and musculature of the viscera including the pharynx, heart and blood vessels. In function they are secretory, visceromotor and vasomotor.

The **somatic motor components** are the motor nerve fibers that supply the striated muscles of the body. In function they are locomotor.

These nerve components from whatever nerve they come make homologous connections in the central nervous system, giving it a columnar arrangement. Within the nervous system the columns bear the same name as the nerve components which are connected with them. As defined by Johnston, a given functional division consists of all the peripheral end-organs belonging to a given type, the nerve fiber components which connect them with the brain, and the brain centers in which these components end or take origin. In the oblongata of Fishes in general, several such functional columns are readily recognized (fig. 279).

The **somatic sensory column** is connected with general sensory, cutaneous, vestibular and lateral line nerves. In the bulbar region the column is formed by the crest or lateral line lobe, the acoustic tubercle and the descending root and nucleus of the trigeminus. The column is indicated in figure 279, *B*, *C*, and *D*, by horizontal lines.

The **visceral sensory column** or visceral lobe is connected with the nerves of taste and visceral nerves. In the bulbar region the column is formed by the centers of the sensory seventh, ninth and tenth nerves which bring in taste and visceral sensibility. This column is indicated in figure 279 by oblique lines.

The **visceral motor column** contains the cells that give origin to motor fibers which supply the viscera. It is small but can be recognized in cross sections just medial to the visceral sensory column (figs. 281–283, *mv*). Its cells give origin to the visceral motor fibers of the seventh, ninth and tenth nerves. In figure 279 the position of this column is indicated by black rectangles. The nucleus of the facial and masticator nerve belong to this column. In some Fishes as well as in higher forms a portion of the facial nucleus migrates laterally in line with the masticator. This is also true of the ambiguus in higher forms. Thus a second visceral motor column is formed dealing with the movements of the mandible, hyoid arch region and the pharynx.

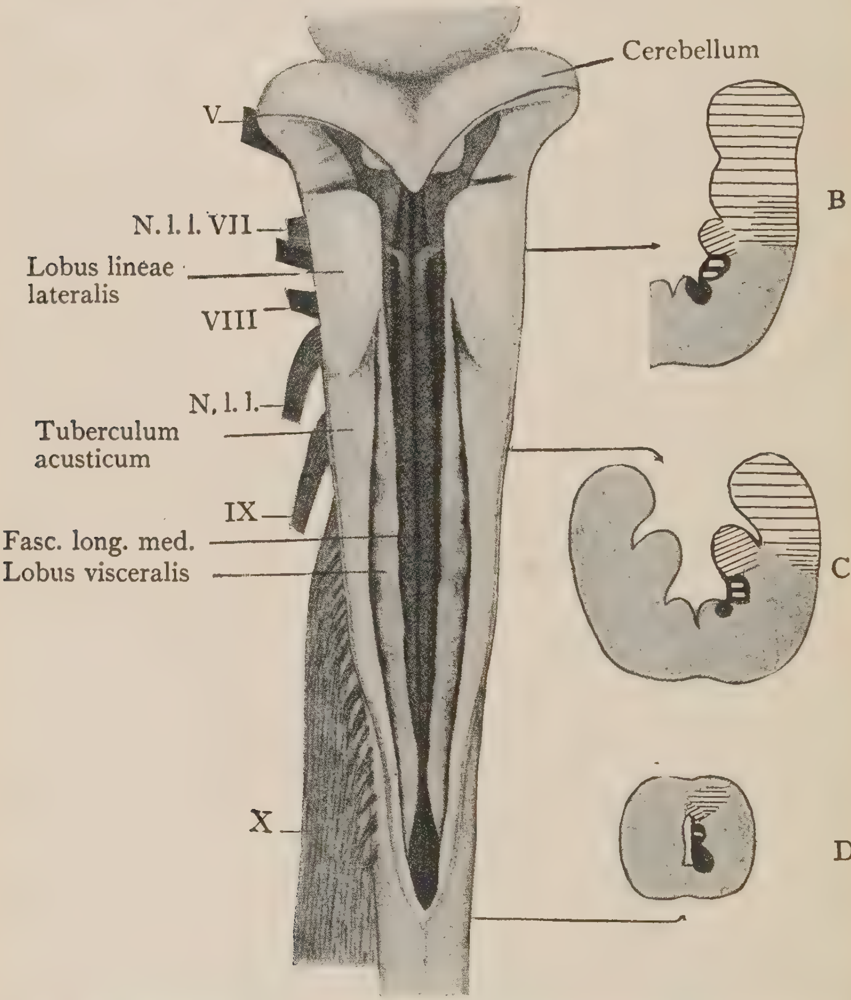

FIG. 279. Oblongata of lake sturgeon, Acipenser rubicundus, showing the longitudinal zones, × ¼. *B*, *C*, and *D* sketches of sections at levels indicate the somatic sensory column, oblique lines the visceral sensory, black rectangles visceral motor, and solid black the somatic motor column, in which end the corresponding nerve components shown in figures 274, 288, and 299. From J. B. Johnston.

The **somatic motor column** of cells lies in close relation to the conspicuous median longitudinal bundle of fibers (*mlf*). These cell groups give origin to motor fibers that supply the ocular and ventral pharyngeal muscles. Their position is indicated in black in figure 279.

The functional columns and the central connections of the cranial nerves can be best shown in sections of a shark (figs. 280 to 285) or some other simple form. In Teleosts (figs. 286, 287) various parts of the brain are highly specialized and there is, in most species, a greater compactness and distortion of the primitive alignment seen in the sharks and the sturgeon.

The **somatic sensory column** forms the dorsal margin of each side of the oblongata. It is made up of the cellular masses in which end the roots of the lateral line (*l*), vestibular (*vn*) and trigeminal (*t*) nerves. These are all cutaneous sensory nerves. The dorsal border is formed by the nucleus of the lateral line, called the acoustic tubercle. Where it joins the cerebellum it is covered by a cellular crest (*cbc*) which forms an ear-like appendage on each side (fig. 275) and then passes to the midline under cover of the posterior lobe of the cerebellum. It is considered as representing a primitive flocculus (Kappers).

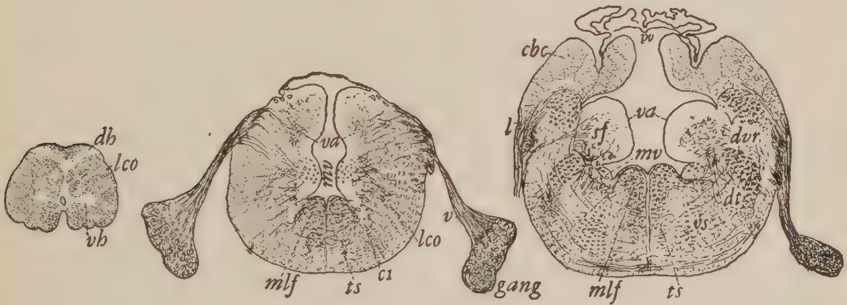

Fig. 280. Section of cervical cord of spiny dogfish, *squalus a*, × 10.
Fig. 281. Section of lower oblongata of *squalus a*, × 10.
Fig. 282. Section of middle oblongata of *squalus a*, × 10.

The **lateral line nerves** are three in number:

1. The lateral line component of the trigeminus and hyomandibular (facial) is the large anterior one. It supplies the lateral line and ampullary organs in the head region. It arises from large ganglia associated with those of the trigeminus and hyomandibular (facial). It enters the acoustic tubercle by a large dorsal root (fig. 284, *l*), and also by a ventral root associated with the vestibular root. The two roots are seen in acanthias (figs. 275, 276). The large ves-

tibular root is seen entering the ventrolateral side (fig. 284, *vn*). The lateral line enters through a fold in the crest. Its fibers divide in its medial border and become ascending and descending bundles among which the underlying cells are scattered.

2. The lateral line component of the vagus is large. It arises from ganglion cells in relation to the vagal ganglion and its peripheral trunk passes down into the body wall to supply the long series of lateral line organs on the side of the body.

3. The lateral line component of the glossopharyngeal is small and supplies the lateral line organs of the temporal canal. The central roots of these nerves enter the posterior part of the nucleus of the lateral line (fig. 282, *l*) and pass upwards through it.

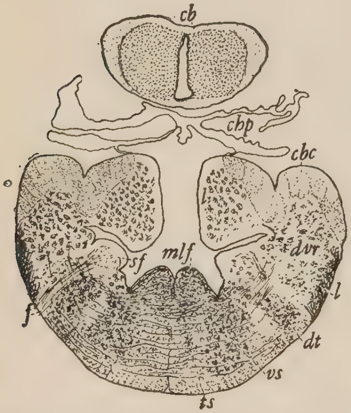

FIG. 283. Section of upper oblongata of *squalus a*, × 10.

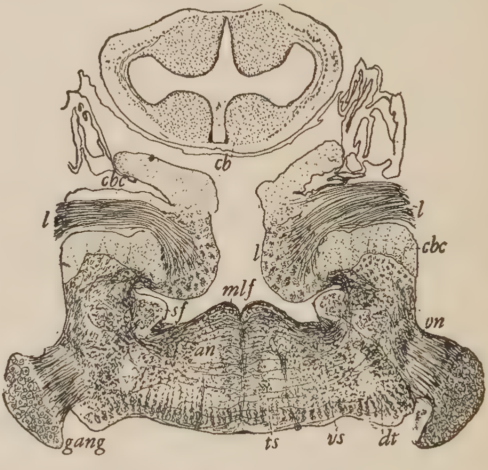

FIG. 284. Section of same at entrance of dorsal lateral line, × 10.

The **vestibular nerve fibers** arise from a large ganglion medial to the vestibule. For the structure of the vestibule see Retzius' "Gehororgan." The peripheral branches of the nerve supply the end organs in the ampullae of the three canals, in the saccule and utricle. The central fibers enter the vestibular area as two roots. The dorsal root bifurcates, the ascending branches entering the cerebellum (fig. 285). The descending branches pass down in the vestibular area ventral to those of the anterior lateral line. The ventral branch enters on a more ventral level and descends to end in the lower part of the vestibular area.

The **central connections** of the lateral line and vestibular area are complex and as well developed in Fishes as in higher forms. The function of the vestibule has been shown (by Maxwell and others) to deal with the movements of equilibrium and the maintenance of body posture and eye movements. The function of the lateral line organs has been shown to be the reception of vibrations in water (Parker). These appear to exercise an inhibitory influence on movements (Lee) and may be compared to the inhibitory functions of the vestibular centers in higher vertebrates. A true auditory organ or cochlea of higher forms has not been differentiated in Fishes, although a fiber connection with the tectum is probably the forerunner of the lateral lemniscus of higher forms.

From the vestibular nuclei arcuate fibers cross the midline and enter the medial longitudinal fasciculus (fig. 289, *mlf*), the larger part of which they form. The bundle ascends to end in the trochlear and oculomotor nuclei which supply the ocular muscles and descends to end in the ventral horn cells of the spinal cord. Fibers also pass directly into the abducens nucleus. Other fibers pass without crossing down into the spinal cord. To these simple reflex systems there are added, in the adult fish, fibers from the cerebellum that not only end in the vestibular and lateral line nuclei but pass up and down with the vestibular tracts and may make connections with the reticular nuclei. One such bundle comparable to the brachium conjunctivum of Birds ascends to the region of the oculomotor nucleus. Another large bundle comparable to the acoustic stria of Birds (fig. 242) arises from the lateral line nucleus, crosses the midline and then passes up in the other side to the lateral nucleus in the posterior part of the tectum. This is comparable to the lateral lemniscus, but is, in the Fishes, the lateral line optic connection. A diagram of the connections of these centers is shown in figure 289.

The **trigeminus nerve** (*t*) enters the lateral surface at the upper end of the oblongata and its root (*dt*) descends in ventral relation to the lateral line and vestibular roots (figs. 282–285). It ends in a columnar nuclear mass along its course. It is a general cutaneous sensory nerve to the head region. Its function is believed to be tactile. The central columns formed by the roots of the trigeminus, vestibular and lateral line nerves form the **somatic sensory column** of Johnston, indicated by horizontal lines in figure 279, *B*, *C*, *D*. These structures are more strongly developed in the bony fishes.

The **visceral sensory column** is seen on the inner surface as the visceral lobe (fig. 279). In the dogfishes (fig. 275) it forms a lobulated ridge developed around the entering roots of the visceral sensory components of the facial or hyomandibular (*f*), glossopharyngeal (*gn*) and vagus (*v*). General sensory fibers with free endings from the visceral and gill regions also enter through these

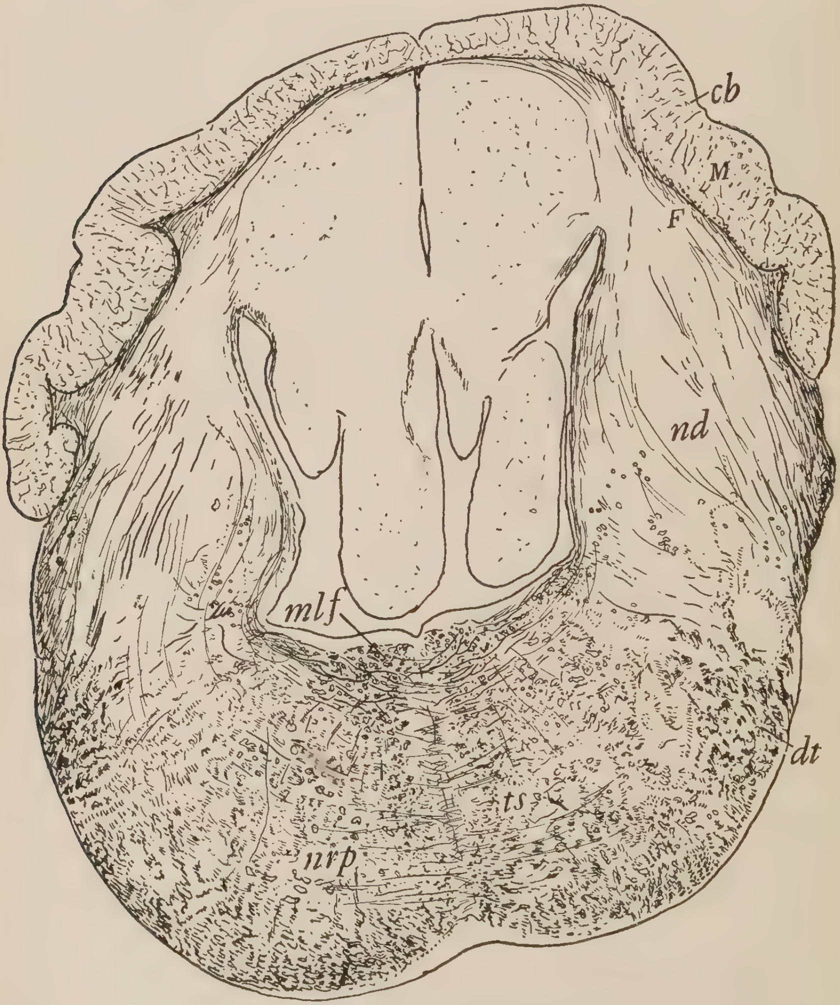

FIG. 285. Section through the cerebellar region of a ray, *raja b*, × 9.

three nerves. The last two are distributed to the viscera and gill region; the facial supplies the hyomandibular region in front of the gills. The nerves also carry gustatory fibers that supply the taste buds in and about the mouth and on the barblets of such siluroid fishes as the bullheads and catfish. In many of these forms in whom the taste buds are numerous the taste components are large and there is a corresponding overgrowth of the vagal lobes (Herrick) which protrude dorsally and may reach great size as in the buffalo fish (figs. 286, 287). In such forms large gustatory tracts arise from these lobes and pass to a secondary gustatory nucleus in the midbrain.

In the dogfish (figs. 281–284) this visceral sensory column is seen as a cellular ridge (*va*) occupied in part at different levels by a bundle of root fibers of the sensory facial, glossopharyngeal and vagus nerves. These root fibers form a common bundle known as the fasciculus communis or solitarius (*sf*) and end chiefly in relation to the small cells that form the ridge-like elevation. These constitute not only the visceral and respiratory but also the taste centers.

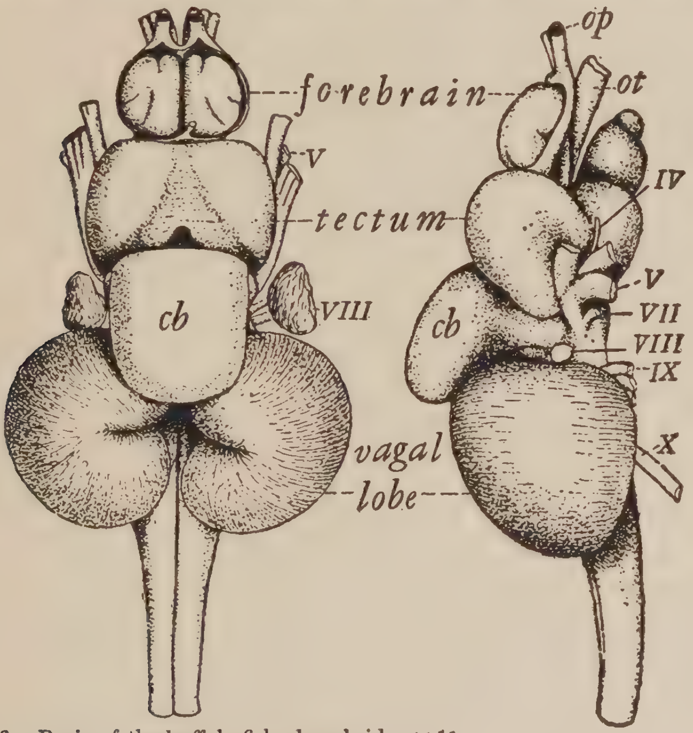

FIG. 286. Brain of the buffalo fish, dorsal side, × 1½.

FIG. 287. Same brain seen from left side. From C. J. and C. L. Herrick. The taste buds and nerves are greatly developed. As a result the vagal lobes are of great size. The facial are smaller and are concealed by the cerebellum. The optic lobes (*tectum*) are distended by the large valvula of the cerebellum which occupies their ventricle. The various nerves are indicated by Roman numerals. For nerve components in Bony Fishes see figure 288.

They make important short connections with the adjacent visceral motor centers (*mv*).

The **visceral motor column** is one of large motor cells, which supply the glands and muscles of viscera and at higher levels also the muscles of the gill arches, of the hyoid region and mandible.

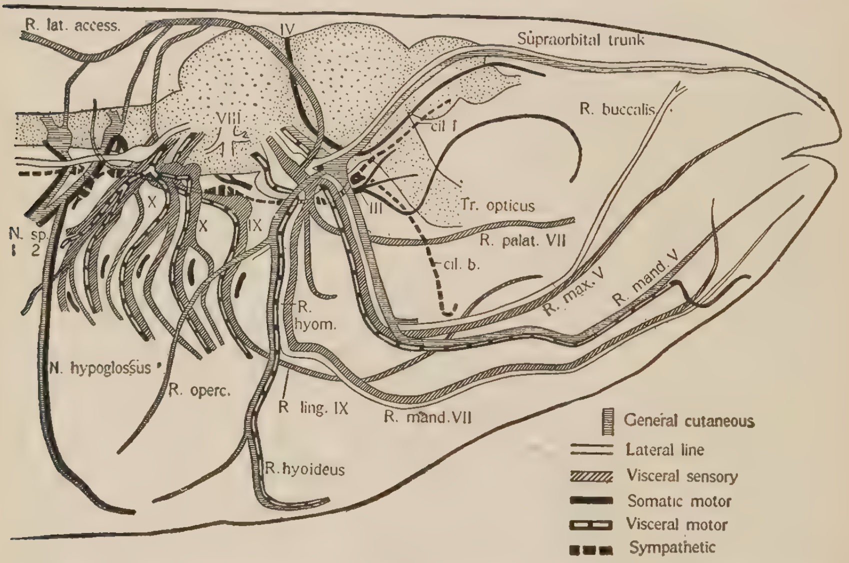

FIG. 288. The functional components of the cranial nerves of a bony fish, *menidia*. From J. B. Johnston, after reconstructions of C. J. Herrick.

This group of cells (*mv*) is situated ventral and close to the visceral sensory column. A separation into a laterally situated ambiguus group does not occur in Fishes.

The respiration of Fishes is done by rapid movement of the gill arches which draws in water through the mouth and expels it through the gill clefts, thus areating the blood which perfuses the inner vascular gills. In the bony fishes the hyomandibular and opercular muscles take the important part. This is a rapid, rhythmic muscular movement necessary to the life of the fish. It is activated chemically by the presence of carbon dioxide in the blood. The muscular coördination and movement are, however, accomplished by neural arcs. The distribution of the visceral nerves to the gills is shown in figures 274, 288, 299, IX, X.

The intake and selection of water and food is also effected by neural arcs through the facial (*R. hyom.*) and masticator (*R. mand.*

V) nerves. These are reached by special tracts from the gustatory centers and from upper regions of the brain.

The **somatic motor column** of cells is represented by the abducens nucleus situated against the medial longitudinal fasciculus (fig. 284, *an*). In the midbrain region it is represented by the trochlear and oculomotor muscles. Their chief innervation is from the vestibular centers through the median longitudinal fasciculus (*mlf*) and from the optic centers in the tectum and midbrain.

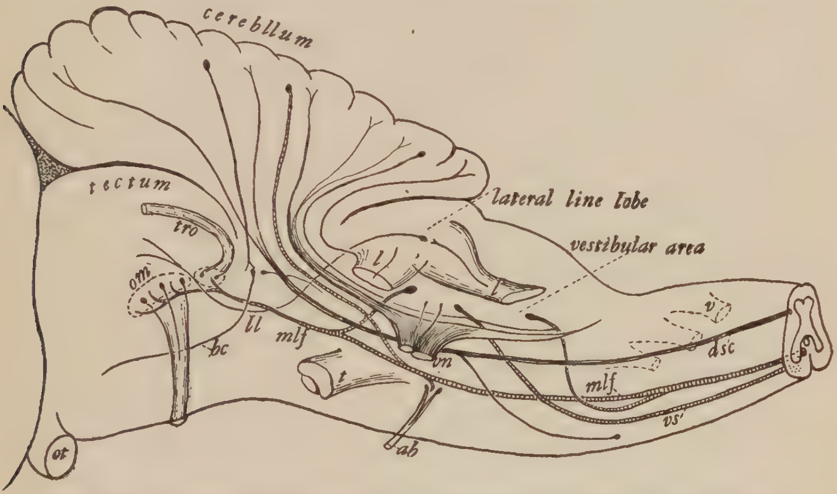

Fig. 289. Diagram of vestibular and cerebellar connections in a dogfish.

In the reticular formation of the oblongata occur groups of scattered cells which form the reticular nuclei and appear to give off descending fibers. The nerve roots, lateral line, vestibular and cerebellar fiber systems dominate the picture. Ascending tracts from the cord reach the cerebellum and tectum opticum. The chief descending tracts appear to be the vestibulospinal tracts, the tectospinal tracts from the optic tecta and the reticulo-spinal tracts.

The **cerebellum** of sharks and rays is a median structure. It shows a considerable advance in development over that of the Cyclostomes, Amphibia and Reptiles. In the spiny dogfish (figs. 275, 276, *cb*) it is still a small median structure developed over a large ventricle. In the smooth dogfish (figs. 277, 278) it is large and strongly fissured in a transverse direction. Its cortex is also well developed (fig. 285) and shows a differentiation into an outer molecular layer (*M*), a layer of large Purkinje cells (*Pc*), a fiber layer (*F*) and an internal granular layer (*G*).

The cerebellar crest (*cbc*) that covers over the appendages of the lateral line lobe may be considered as a cerebellar structure forming a primitive floccular lobe.

The cerebellum of the bony fishes (Teleosts) is more compact, crowding out the cerebellar ventricle (figs. 286, 287). It is never conspicuously fissured as in the Selachians. Instead of overlapping the midbrain as in the dogfish (figs. 277, 278) the anterior lobe of the cerebellum which is strongly connected with the tegmentum of the midbrain is thrust into the ventricle and in sections appears on the inside. The manner of this intrusion can be seen in a median section (fig. 290). In the Teleosts the optic lobes (tecta) are strongly developed and extend backwards over the anterior lobe of the cerebellum. The membrane which joins the tectum to the cerebellum is converted into cerebellar tissue, and in some Teleosts it becomes greatly folded, forming the valvula cerebelli, inside of the tectum.

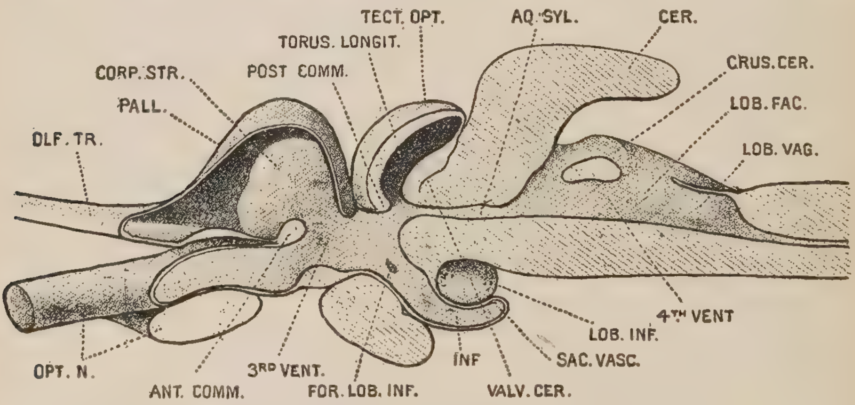

FIG. 290. Brain of a codfish, *Gadus Morrhua*, in sagittal section. From G. E. Smith, Cat. mus. Roy. Coll. Surg. Eng.

The afferent fibers to the cerebellum are root fibers of the vestibular nerve, a spinocerebellar tract, fibers from a rudimentary inferior olive, a large tecto-cerebellar tract, and a lobo-cerebellar tract from the hypothalamus. The chief efferent fibers enter the vestibular nuclei and join the vestibular tracts. Their function is probably a synergic one exercised through the vestibular tracts. They are said to be in direct connection with the nuclei of motor nerves, which is not the case in higher vertebrates. A smaller efferent connection similar to the brachium conjunctivum passes forward to end on large cells in the base of the midbrain and in the hypothalamus through which it becomes linked with the forebrain.

The **midbrain** is distinguished by the large optic lobes or **tecta** on its dorsal side in which the fibers of the optic nerves terminate. In Teleosts they attain a greater size and importance then in the Elasmobranchs. They are oval in form and are separated by a longitudinal groove. They contain a large common cavity or midbrain ventricle. In the Teleosts this is invaded by the valvula of the cerebellum and becomes greatly expanded. In the Sharks the anterior lobe of the cerebellum overlaps the tectum and the valvula is not intruded into the ventricle to any such extent.

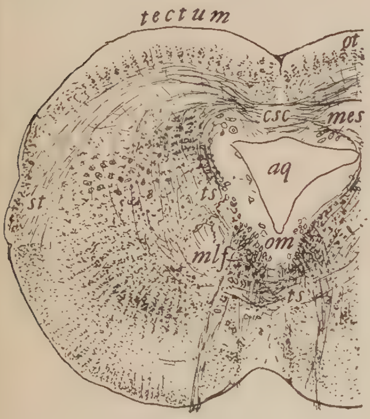

FIG. 291. Section through the midbrain of a ray, × 9.

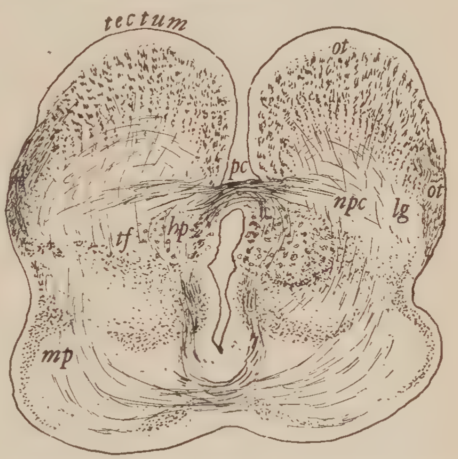

FIG. 292. Section through the anterior part of the midbrain of a ray, × 9.

In structure the tectum of Fishes may be taken as a prototype of the tectum of other vertebrates (fig. 291). It is a thick rounded wall of cellular structure penetrated by a stratum of optic fibers (*ot*). From the lateral side it receives also the fibers of a large spino- and bulbo-tectal tract (*st*). From the cellular layers there arise arcuate fibers that pass to the midline and connect with the oculomotor nuclei. A portion of these fibers forms the large tecto-spinal tract (*ts*) which crosses the midline and passes down ventral to the medial longitudinal fasciculus (*mlf*). A commissure of fibers unites the tecta on the dorsal side (*csc*). Here are seen the large globular cells (*mes*) that give origin to the mesencephalic root of the trigeminus nerve. In the posterior part of the tectum there is found a cellular mass, in which terminates a bundle of fibers from the lateral line nucleus. This region is comparable to the inferior colliculus of higher forms. The optic tectum is the important visual center upon which the various parts of the retina are directly projected. Correlated with vision are sensory impulses, probably tactile or kinesthetic, brought in by the bulbotectal tract.

The **tegmentum** is the term applied to the base of the midbrain. It contains a number of tracts and the important oculomotor centers and their connections. The oculomotor nuclei (*om*) are located near the midline ventral to the aqueduct. Caudal to them are the torchlear nuclei. These motor cell groups give origin to nerves that supply the eye muscles. The oculomotor is the largest and most complex. Its fibers pass out through the ventral side. The trochlear is smaller and its fibers pass out dorsally by crossing through the velum that joins the cerebellum to the tectum. The medial longitudinal fasciculus (*mlf*), chiefly of vestibular origin, ends in relation to these motor nuclei. Fibers from the tectum also end here; and fibers from the posterior commissure end close by in the interstitial nucleus which contributes fibers to the medial longitudinal bundle.

In the ventral region, too, there occurs a diffuse reticular mass of cells, the homologue of the reticular and red nuclei of higher forms. In this there ends a bundle from the forebrain and one coming from the cerebellum, probably the homologue of the brachium conjunctivum. A transverse commissure as in higher forms is found back of the optic tracts connecting the posterior regions of the tecta.

The **thalamus** in Fishes is a narrow segment which connects the midbrain to the forebrain. Except in the posterior part (fig. 292) it is undeveloped (fig. 293). It corresponds most closely to the ventral or subthalamus of higher forms and on its under side it projects back of the crossing of the optic tracts as the tuber or hypothalamus which ends in a large vascular sac. A dorsal sensory thalamus in connection with the midbrain is slightly developed in Fishes. Three features deserve special comment, the optic connections, the forebrain bundles, and the hypothalamic connections (fig. 294).

The **optic tracts** coming from the retina cross totally ventral to the thalamus (*tr. op.*). Their termination is in the tecta. But, as they pass over the surface of the thalamus they give off branches to the pretectal and lateral geniculate nuclei (fig. 292, *lg*). From the pretectal region fibers of the posterior commissure (*pc*) take origin, cross the midline and turn down to end in the interstitial nucleus at the upper end of the medial longitudinal fasciculus, above oculomotor nucleus. This is an arrangement common to most vertebrates.

The **geniculate body** (fig. 292, *lg*) receives collaterals from the optic tract and sends fibers to the somatic striatum (fig. 295, *a. som.*). The region medial to the geniculate body (fig. 292) receives spino- and bulbo-thalamic fibers and likewise projects fibers on the somatic striatum (*tf*). This region together with the geniculate body forms the rudiment of a sensory thalamus. The somatic area with which they connect is probably the homologue of the older parts (the amygdala) of the somatic striatum of higher vertebrates. It should be noted that this area projects a striopeduncular tract (*tr. som. p.*) downwards to the masticator and facial nuclei which innervate the hyomandibular muscles. It is also called the lobobulbar tract in Fishes. A striothalamic connection also exists as a large fiber tract that connects the more anterior parts of the striatum (*a. ol. l.*) with the tegmental region surrounding the oculomotor nuclei. The habenular bodies are well developed and receive fibers from the forebrain and connect by the habenulopeduncular tract with the interpeduncular region. This is a system constant in all vertebrates.

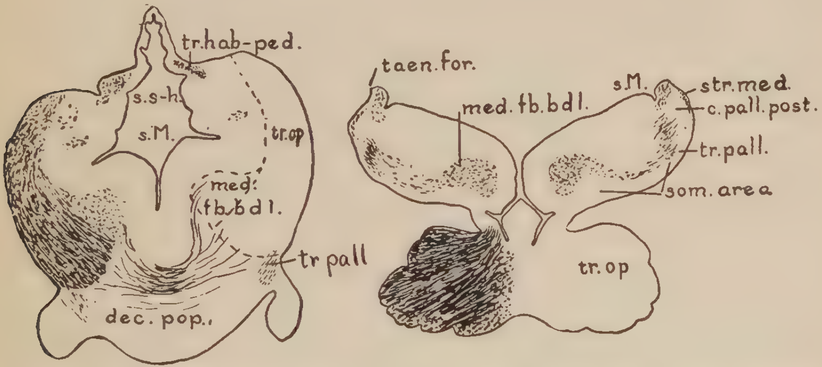

FIG. 293. Sections through the thalamus of a dogfish, *s. acanthias*. From Johnston.

The **hypothalamus** in Fishes is highly developed and is connected at its caudal end to a vascular sac. In Sharks the sac is lined by a sensory epithelium which sends fibers to a small ganglionic mass in the hypothalamus. In front of the chiasma in the medial wall is the preoptic nucleus (paraventricular of mammals) which sends fibers to the blood vessels of the vascular sac and the pituitary gland. In mammals the basal optic nucleus occurs in a more ventral position, and in Primates a large nucleus tuberis lateralis is developed (Malone).

The fiber connections of the main portion of the hypothalamus (tuber) of a dogfish are shown in figure 294. It will be seen that two way connections exist between the walls of the tuber and the medial and dorsal olfactory areas of the forebrain. These tracts form the medial forebrain bundle (*f. med. t.*) which, as in all vertebrates, connects the medial and ventral regions of the forebrain with the hypothalamus. In a similar way the ventral lateral wall including the striatum is connected with the peduncular region by the tracts that constitute the lateral forebrain bundle.

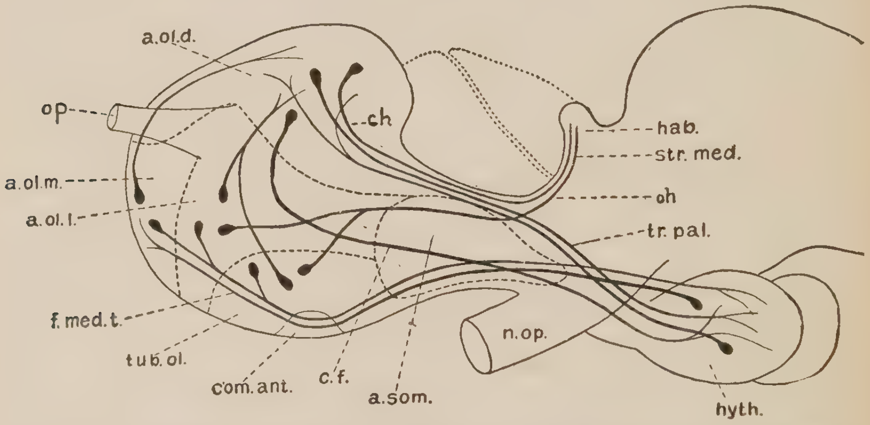

FIG. 294. Diagram of forebrain of Acanthias seen from the left side illustrating some of the connections of the olfactory area. From C. J. Herrick, Libro en honor de Cajal. Based on figures and descriptions of J. B. Johnston.

A mammillary peduncle also exists which enters the lateral side of the posterior portion of the large tuber. Fibers connect this region with the diffuse subhabenular region or anterior nucleus of the thalamus.

The **forebrain** of Fishes is almost wholly an olfactory organ. The olfactory cells that constitute the two sense organs of smell have, by contact with the rostral end of the brain tube, caused a great development and bilateral outpouching of its walls. In the Cyclostomes (fig. 298), Selachians (figs. 275–278) and Ganoids this process of bilateral outpouching of the forebrain vesicle is still in its initial stages. Much of the forebrain still remains unevaginated as the median endbrain. For this reason the forebrain and lateral ventricles of the Elasmobranchs are not exactly comparable with the more fully evaginated forebrain vesicles of the Amphibians (fig. 261) and higher forms. The fore end of each vesicle or olfactory bulb (*ob*) remains in contact with the olfactory sac from which it receives the fibers of the olfactory cells. In some Elasmobranchs (fig. 296) the bulb remains in close connection with the hinder part of the vesicle or olfactory lobe. In others as in the dog fishes (figs. 275–278) the connection becomes elongated into a hollow stalk, the olfactory peduncle (*op*). Through the walls of the peduncle olfactory tracts pass back to end in the walls of the lobes (fig. 295, *tr. ol.*), all of which receive these secondary olfactory fibers.

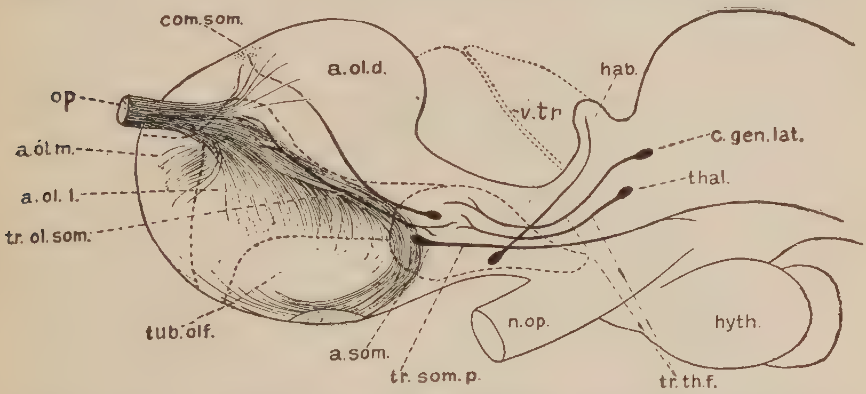

Fig. 295. Diagram of forebrain of Acanthias, illustrating connection of the somatic (striatal) area. From C. J. Herrick, based on figures and descriptions of J. B. Johnston.

The lateral walls are united through the ventral side of the median unevaginated portion by means of fibers that form the anterior commissure (*com. ant.*). The medial or septal walls of the forebrain vesicles are united by a thick terminal lamina, and an extensive thickening of their medial walls and lamina may take place as in the smooth dogfish (figs. 277, 278) in which the lobes are completely fused. In the ventral wall of each lobe is differentiated the olfactory tubercle (*tub. ol.*) and its nucleus, which forms a fundamental landmark in forebrain morphology.

In the walls of the forebrain two longitudinal zones are recognized (figs. 294, 295). The medial zone consists of a septal or medial olfactory area (*a. ol. m.*), a ventral olfactory area or olfactory tubercle (*tub. ol.*) which joins the preoptic region. Its fiber connections are through the medial forebrain bundle (*f. med. t.*) with the hypothalamus, and with the habenular nuclei by means of the olfactohabenular tract (*str. med.*). These olfactory areas also send fibers to the dorsal olfactory area (*a. ol. d.*). These fiber connections resemble those seen in the brains of higher vertebrates as has been shown by Johnston and Herrick. The resemblance is closer than is generally supposed.

The lateral zone consists of a dorsal olfactory area (*a. ol. d.*) which includes the primordium hippocampi of Johnston, and a lateral olfactory area (*a. ol. l.*) connected backwards by means of a somatic striatal area (*a. som.*) with the wall of the thalamus. The dorsal area is connected with the hypothalamus by means of the tractus pallii (fig. 294, *tr. pal.*) and by the corticohabenular tract (*ch.*) with the habenula. The somatic area (*a. som.*) is a forward continuation of the thalamic wall with which it is in connection by means of thalamic fibers (*tr. th. f.*) from the geniculate body and medial thalamic nuclei. The striatal region is connected forward with the lateral olfactory area by the olfacto-somatic tract (*tr. ol. som.*) which is reminiscent of the corticoepistriate (*cst.*) tract of Birds and Reptiles. Striothalamic as well as striopeduncular tracts (*tr. som. p.*) make important downward connections. The ventral regions are connected by the anterior commissure (*com. ant.*). The dorsal or septal walls are united by the septal or anterior pallial commissure which passes through the thick septal region (fig. 305, *c. pall. ant.*). Johnston ('11) and Holmgren ('22) have recognized in the dorsal

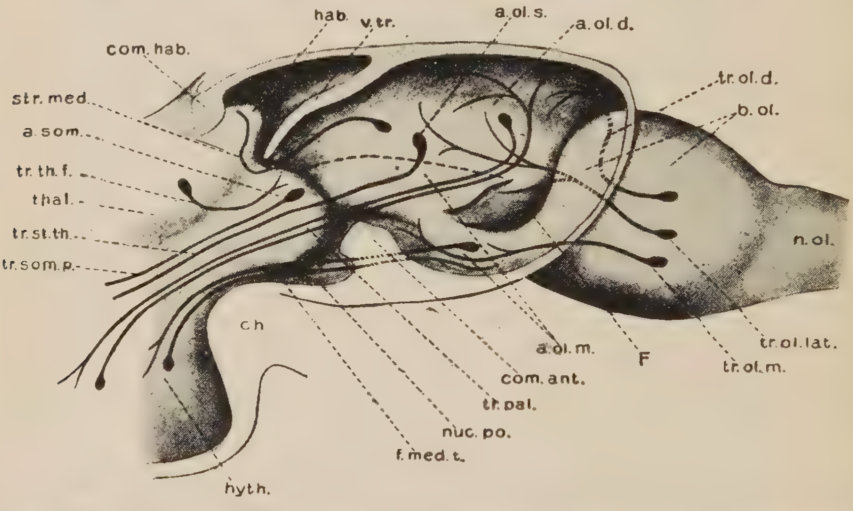

FIG. 296. Median section of forebrain of a bony fish, amia calva. The main tracts are drawn in to indicate their position and connections. From C. J. Herrick, based on work of J. B. Johnston.

olfactory area a primordium hippocampi (*prim. hipp.*) back of this commissure. The structure of the Elasmobranch brain is on the whole primitive and not so divergent from the main vertebrate line as is that of other Fishes. A comparison of a typical section through the forebrain of a dogfish with that of a frog (fig. 306) shows a fundamental similarity in cell structure. In its essential features the Elasmobranch brain and fiber connection has followed a line of evolution which makes it quite comparable to the forebrain of Cyclostomes, Amphibians and Reptiles.

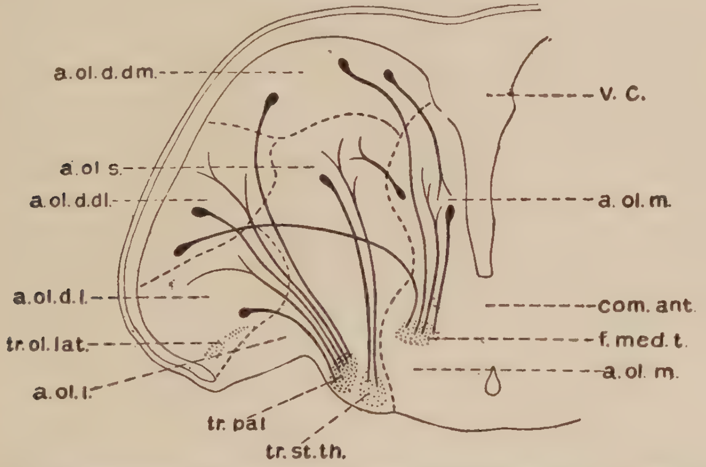

FIG. 297. Diagrammatic cross section through the forebrain of the carp, *Cyprinus carpio*, at the level of the anterior commissure outlining the several areas and showing their fiber connections. From C. J. Herrick. Libro en honor de Cajal.

The **forebrain of bony Fishes** (Ganoids and Teleosts) differs from that of the sharks in the great thickening and compactness of its ventral and lateral walls which produces their eversion and a thinning out of the dorsal wall into a membranous roof (figs. 290, 296). Medial, dorsal and lateral olfactory areas (fig. 297) are concentrated around a central somatic area (*a. ol. s.*) so that the basal structure as a whole begins to resemble a striatum. These structures appear in the lateral walls. Their earlier relations to the medial wall can be seen in figure 296 which shows the conditions in a more primitive form. A septal region is not formed but the basal regions become more closely united with the lateral and an inversion of the various areas takes place.

The medial area (figs. 296, 297, *a. ol. m.*) is connected with the hypothalamus by means of the medial forebrain bundle (*f. med. t.*).

It receives as in the Sharks connections from the dorsal medial area (*a. ol. d. dm.*). The whole lateral surface is connected with the hypothalamic and peduncular regions by the tractus pallii (*tr. pal.*) while the central region (*a. ol. s.*) is connected downwards by the striothalamic tract (*tr. st. th.*). All of these regions are reached by secondary olfactory fibers (*tr. ol. lat.*) from the bulb and by fibers from the hypothalamus. Other sensory connections with the thalamus are weakly developed.

It appears that in the Fishes in general the gustatory sensations reach the hypothalamus and are projected forward on the olfactory centers. The forebrain of Fishes may therefore be regarded as a center for the correlation of taste and smell and the initiation of appropriate ocular, hyomandibular (opercular) and feeding movements. Spatial orientation is probably a tectal function, while equilibrium and the static and kinetic functions are probably vestibular and cerebellar.

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CHAPTER 38

The Brains of Cyclostomes

The Lampreys are the most ancient aquatic forms with a true vertebrate organization of the head region. They are no doubt closely related to the ancestral forms of Fishes. The modern fishes (Elasmobranchs, Ganoids, Dipnoi and Teleosts) have already a highly advanced nervous system which possesses in its reflex patterns most of the fundamental structures common to Amphibia, Reptiles, Birds and Mammals.

The brain of the primitive fish-like Lamprey, Petromyzon, may be taken to illustrate that of the archaic Fishes now long extinct. It resembles on the one hand the brain of the surviving primitive Fishes (Elasmobranchs, Ganoids and Dipnoi) and on the other hand that of Amphibians. Moreover, it shows many primitive conditions of development and structure. The larvae of the Lampreys grow up in seclusion in mudbanks along streams, where they lead an inactive life (S. H. Gage). The adults develop a large round suctorial snout from which they get the name of cyclostomes. By means of this organ they become attached to objects or other fish; and some lead a parasitic life. This accounts in part for the shortness of the forebrain, the peculiar position and mode of perfusion of the olfactory organs, the special rasping and suctorial organs of the mouth and the peculiarities of the vestibule.

The spinal cord is flat and ribbon like. The gray matter has not differentiated into the dorsal and ventral horns typical of other vertebrates. The spinal ganglia which give origin to the sensory nerve fibers are close to the cord, in a partial state of development. Many of their large sensory cells still lie within the spinal cord dorsal to the central canal. The motor nerve fibers arise from cells ventral to the canal. They have a primitive mode of distribution since they alternate with the sensory fibers and do not join them as in higher forms. The dorsal roots and intersegmental fibers from the cord cells form the chief fiber systems. Some of the latter probably ascend to the oblongata and cerebellum and others descend from the large reticular cells of the oblongata and midbrain.

The brain is relatively small and with the exception of the oblongata shows a low stage of development (fig. 298).

The **oblongata** or bulb forms a larger part of the brain than that in other fishes. In form it resembles that of Amblystoma (fig. 272). It owes its great development to the central connections of the fifth to the tenth cranial nerves. Its dorsal surface is covered by a well-developed vascular membrane which roofs over the fourth ventricle.

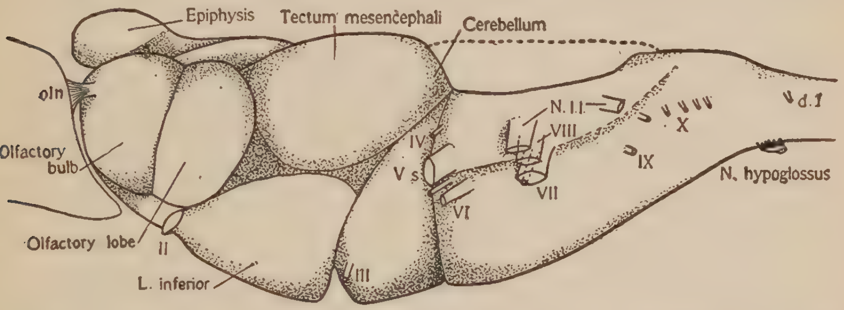

FIG. 298. A sketch of the brain of a Cyclostome fish, *Lamptera Wilderi*, as seen from the left side. From J. B. Johnston.

As in Amblystoma (fig. 273) the cells retain a primitive central position while the roots and tracts form the outer structure of the walls of the oblongata.

The **cranial nerves** are highly differentiated (fig. 299). Their central connections are indicated in figure 300. It will be seen that their fiber components have the typical visceral and somatic sensory, and visceral and somatic motor distribution, as in all vertebrates. The sensory fibers arise from incompletely differentiated sensory ganglia. The region dorsal to the gills is supplied by the spinal nerves. The nerves are indicated by Roman numerals.

The gill region and its taste buds are supplied by branches of X, IX and VII. The hyomandibular region is also supplied by the VII. Their central connections are with the visceral sensory column or vagal lobe, in which the sensory fibers form a primitive fasciculus solitarius system. Medially, and ventral to the vagal lobe, is the visceral motor column formed of a common group of cells which give origin to the motor components of the IX and X. These nerves constitute a respiratory and swallowing mechanism.

The vestibule is of peculiar form in Cyclostomes (Retzius) possibly due to their parasitic mode of life. It is supplied by the eighth (VIII) nerve whose central connections are by means of two roots in the ventral part of the lateral line lobe. Both roots have ascending and descending branches. From the large cells (of Müller) in this region arise the chief descending fibers that end in the cord. They form the primitive reticulospinal tracts. Lateral line components are associated with the fifth (V), seventh (VII), ninth (IX) and tenth (X) nerves. They supply the lateral line sense organs which have a more primitive structure than in higher fishes. The lateral line nerves enter the lateral line lobe close behind the cerebellum. This lobe is covered by a cerebellar crest. Some fibers of the lateral line and vestibular nerves enter the cerebellum. The **cerebellum** is extremely rudimentary and is chiefly a continuation of the lateral line lobe and its crest. The structure of these is a primitive one, consisting of an inner layer of granule cells, primitive Purkinje cells and a thin molecular layer on the outer surface. The absence of sustained swimming efforts and the parasitic mode of life and migration have not favored a greater development of these tonic and motor regions of the brain.

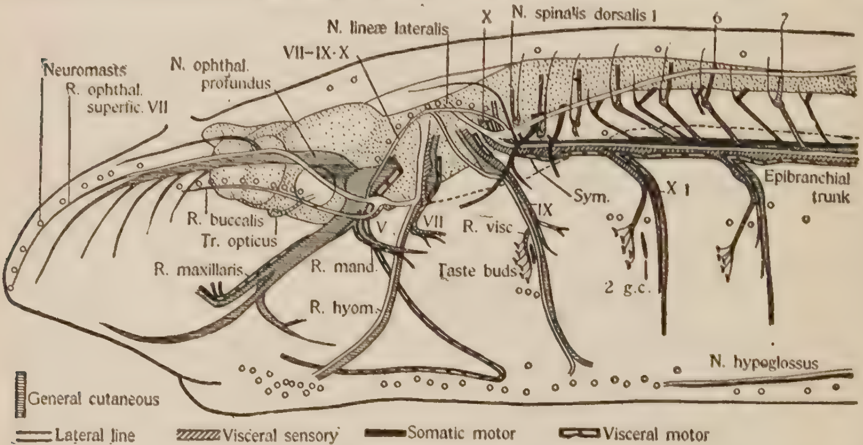

FIG. 299. A reconstruction of the cranial nerve components of a Cyclostome fish, *Petromyzon dorsatus*. Sym., sympathetic trunk; 2 gc., second gill cleft. From J. B. Johnston.

The trigeminus V is strongly developed and with the lateral line supplies the sense organs in the large suctorial snout. Its central root passes down for a long distance in the lateral wall of the oblongata. The central connections of its nucleus are chiefly with the masticator and motor facial nuclei which supply the muscles of the snout, though its caudal terminus may have connections with the spinal occipital nerve centers (for deglutition?). The motor V, or masticator nucleus, and the motor VII are closely associated at the upper end of the oblongata. Their fibers supply the musculature of the snout and the rasping organ. A true tongue in the hypoglossal region is not developed and a true hypoglossus nerve is not present.

The nerves that supply the eye muscles are relatively small (fig. 298). The abducens, or VI, is atypical. It passes out with the masticator and supplies the lateral rectus muscle of the eye and also the inferior rectus which in all other vertebrates is supplied by fibers of the oculomotor. The oculomotor (III) and trochlear (IV) nuclei form a common group in the midbrain and innervate the other ocular muscles.

The **midbrain,** as in other vertebrates, is the chief optic center. The eye is small and poorly developed in the larva but in the adult it acquires more importance. The optic nerve (*ot*) and its central connections in the tectum of the midbrain are less developed than in the Fishes. The tectum is developed chiefly in its frontal and caudal parts. The middle is defective and contains a vascular plexus. Behind and in front of this the tecta are connected by commissures. A posterior commissure (*pc*) with optic and oculomotor connections is present in front of the tectal region as in all true vertebrates. Ascending fibers of bulbar origin (trigeminal? and lateral line) forming a bulbotectal tract (*st*) end in the tectum. This as in other higher vertebrates is probably an opticosensory correlation center for directing the movements of the animal in relation to objects in space. From the tectum a tectobulbar and spinal tract passes down (fig. 300, *ts*). This is another feature common to all true vertebrates. In the ventral part of the midbrain these fibers are intercepted by large reticular cells (of Müller) which send down fibers as in other vertebrates. As in other vertebrates a transverse commissure (*com trans*) joins the lateral sides of the midbrain. It runs back of the optic tracts. A large tract, the mammillary peduncle (*mp*), passes up in the ventral side to end in the hypothalamus. The origin of this fundamental bundle is in doubt in all forms, but it may be a bundle of ascending taste fibers.

Between the tectum and habenular nuclei are inserted the stalks of two small pineal eyes, the fibers of which enter the posterior commissure. These eyelike structures, strange to most vertebrates, occur also in some Reptiles.

The **thalamus** consists of two parts, a dorsal habenular portion (*hb*) and the ventral hypothalamus. Both are linked by fiber tracts with the forebrain as in other vertebrates, although in a simplified way. A vascular sac is not found in Petromyzonts. A commissure occurs back of the tuber.

The **forebrain** is a double, chiefly lateral, evagination, united by a terminal lamina which has a more rostral position than in other vertebrates. Each forebrain vesicle is divided into the frontal part or olfactory bulb (*ob*) which is entered by the olfactory nerve (*oln*) and a caudal part, the olfactory lobe (*ol*). The two parts are separated by a shallow vertical furrow. The forebrain lobes are closely related to the thalamus and pushed back over it by the pressure on the skull of the large suctorial mouth. The bulb sends fibers back to all portions of the lobe (*lot*). In addition, the lobe receives in its dorsal part some fibers from the hypothalamus, the tractus pallii (*pal*), which decussates behind the optic chiasma. The lobes send fibers, the corticohabenular tracts (*ch*), to the habenula (*hb*) and from the ventral side olfactohabenular fibers (*oh*) reach it also. Some of these fibers form a forebrain commissure. From the habenular body the habenulopeduncular tract (*hp*) passes back to the peduncular region. This system is common to the vertebrates. An olfacto-hypothalamic and an olfactotegmental (*olp*) tract extend downwards from the lobes. The latter has a decussation through the anterior commissure which occupies a dorsal position in the

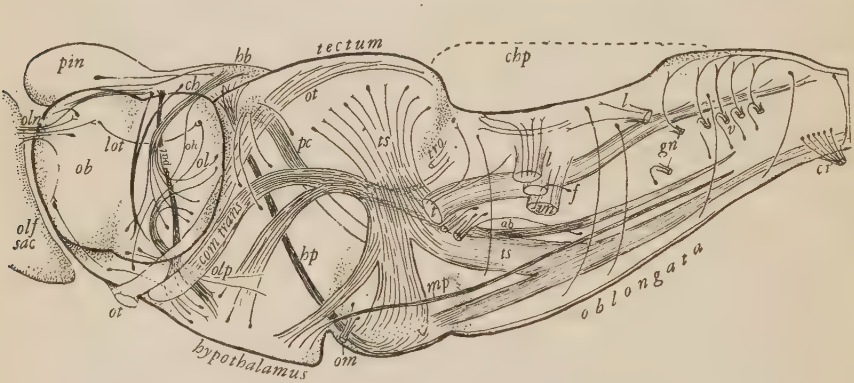

Fig. 300. A plan of the main fiber tracts in the brain of Petromyzon. After J. B. Johnston.

terminal lamina. The thickened olfactory areas and striatal areas of Fishes are not well differentiated in Petromyzonts.

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CHAPTER 39

The Brain of Amphioxus

The Amphioxus is a peculiar prevertebrate form which possesses no true head or special sense organs such as the eyes, lateral line organs or vestibule so distinctive of true vertebrates. It has a narrow elongated lance-like body with closely compacted muscular segments. Its body axis is formed by the notochord, a structure found also in all vertebrates. The front end has a terminal snout or rostrum. Beneath this is an oral opening, and back of this there is a series of lateral primitive gill clefts which communicate with the pharynx.

The brain of Amphioxus is extraordinarily primitive in all parts, although in its embryological development, in its tubular form, in its dorsal position and in its spinal nerve roots it is analogous to that of the vertebrates. In many respects it suggests that the Amphioxus is an ancestral type not far removed from that of the vertebrate line. Its brain may be described as a primitive neural tube comparable in mode of origin and its general form to that of young embryos of all vertebrates.

The nervous system of Amphioxus consists essentially of a small rostral end which may be called the brain and a much larger caudal extension, the spinal cord (fig. 301). It lies over the dorsal surface of the notochord and ends some distance behind its rostral end. It is developed from dorsally placed neural plates of ectoderm which turn up and coalesce to form a neural tube. The anterior end, or neuropore, however, always remains open. In cross section it presents the tubular form with a central slit-like canal characteristic of embryos of vertebrates. The walls of the tube give rise to the nerve cells and fibers. The ventral part of the tube is wide while the dorsal side is narrow, giving the cord a triangular outline in section. In front the tube widens out to form the brain vesicle but no enlargement into brain parts is evident. Figure 301 shows the general form of the nervous system of Amphioxus and the interpretation of its cranial nerves by Kappers.

The **spinal cord** is the longest part, though in development it arises as a caudal extension of the brain tube. It is a bilateral tube with a vertical slitlike canal. Its walls are connected by means of sensory roots and motor roots with the body wall and surrounding myotomes. In number and position these nerves correspond to the septa between the myotomes and consequently alternate on the two sides. No true spinal ganglia are formed and the dorsal root fibers arise from ganglion cells which lie in the dorsal part of the tube close to the central canal. Some bipolar cells occur in the root which may be the beginning of a true extramedullary ganglion cells such as are common to true vertebrates. The intramedullary position of ganglion cells is in true vertebrates found only in Petromyzonts. In the cord the sensory nerves send off fibers which surround large giant cells which lie in the dorsal midline. The axones of these giant cells pass around to the ventral side and form the primitive arcuate or commissural fibers. In the walls of the cord they pass up and down making connections at distant levels. They constitute the chief reflex mechanism of the animal. The origin of the motor fibers is obscure. Apparently they come off as collaterals of longitudinally running fibers. They supply the myotomes and not the visceral muscle. In larval Amphibians Coghill has shown such collateral origin for motor fibers, a single fiber supplying, by bifurcation, the large muscular masses of a myotome. There is in the Amphioxus, as in larval Amblystoma, no evidence of an initial segmental arrangement of neural arcs in the cord. The reflex chaining appears to be longitudinal and chiefly concerned with somatic motor reactions.

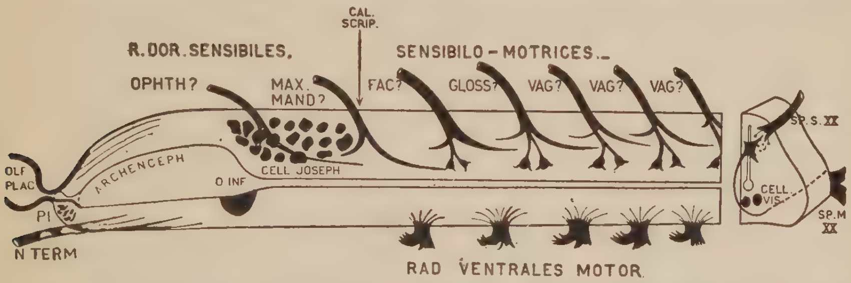

FIG. 301. General plan of the brain of Amphioxus with interpretation of the nerves at the head end. From Kappers' Tabulae Anatomo-comparative Cerebri, Kosmos, Amsterdam.

Special visual cells occur in considerable number ventral to the central canal. They are solitary cells, each covered by a pigment cell for the absorption of light. These pigment cells are dorsal to the visual cell on the right side and ventral to it on the left so that the cells receive their light stimuli from the opposite direction (Boeke).

The **brain** is formed by a vesicle at the front end. A choroid plexus occurs behind the second pair of dorsal nerve roots. This point (*cal scrip*) may be taken to correspond to the roof of the oblongata of vertebrates, though no widening or specialization of its walls has taken place. No vestibular or lateral line nerves occur in Amphioxus and the nerves in this region from the third on may be taken to correspond to the vagal and spino-occipital group since they innervate the region of the primitive gill apparatus.

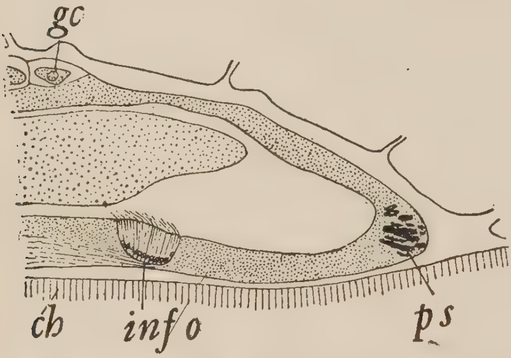

Fig. 302. Median section through rostral end of brain of Amphioxus. From Boeke. *gc*, ganglion cells; *inf o*, infundibular organ; *ps*, pigment spot; *ch*, notochord.

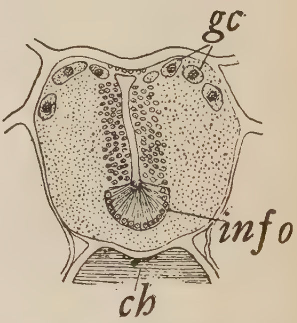

Fig. 303. Section through the infundibular organ of Amphioxus. From Boeke.

A cluster of large cells (*gc*) occurs just in front of the choroid plexus, a region which may be taken to be the primordium of the vestibular and cerebellar centers. The course of their axones and their function is uncertain. This region is connected by the first two pairs of dorsal nerve roots which have been homologized with the ophthalmic (*ophth*) and maxillary (*max mand*) branches of true vertebrates. In the ventral side of the frontal end of the neural tube there occurs a pigment spot (*pl*) which, however, according to Parker, gives no reaction to light. Thus the primordium of a true eye cannot be said to exist and anything like the midbrain region is lacking. The myotomes of the head region are supplied by ventral roots that have a more caudal exit.

The rostral end of the brain is a simple tube connected in front to two terminal nerves. Its front end is closed by a terminal lamina which opens out by the anterior neuropore into a ciliated external pit (*olf plac*). Thus the brain cavity is in free communication with the outside as in early vertebrate embryos. The pit may be taken as the primitive sensory orifice of the neurenteric canal, since it sends fibers into the frontal end of the brain. Lateral olfactory pits are not formed, although a " wheel organ " is present. Ventral to the neuropore is the pigment spot. Boeke has described in the hinder part of the floor, a ciliated sense organ (fig. 303, *inf o*) which is comparable to a similar organ in the vascular sac of lower Fishes. This is a landmark of great morphological value, since a similar structure has been identified in the young embryos of higher animals in a similar position. This region is entered by a pair of terminal nerves (fig. 301, *n ter*) which supply sense cells in the skin of the rostrum or snout. These terminal nerves appear to be homologous with the terminal nerves described by Locy in Selachians (fig. 305). They are found also in other forms with a well-developed rostrum.

Aside from the oral opening and skin nerves and head myotomes the fore end of Amphioxus lacks all typical sense organs and associated neural structures of a true vertebrate. From the point of view of true vertebrate morphology it may be regarded as a nearly headless animal.

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CHAPTER 40

EVOLUTION OF THE FOREBRAIN

The origin of the forebrain of the vertebrates is still a matter of speculation. It has been looked for in the direction of the Amphioxus, Ascidians and Ostracoderms.

The spinal cord of Amphioxus (fig. 301) closely approaches that of the true vertebrates, and at the oral end there is a distended ventricle that bears a resemblance to the oblongata, related as it is to the rostrum and a gill mechanism. There are present rostral nerves comparable to the nervus terminalis. The nerves about the oral opening are comparable to the trigeminus and the nerves to the gill region to the vagal group. There are, however, in the Amphioxus no true eyes or lateral line organs.

Visual organs are a distinctive feature of all true vertebrates and have no immediate relation to similar structures that occur in the invertebrates. They arise as light receptive vesicles in the rostral end of the brain, which eventually separate from the nervous tube and become the eyes. Through the optic nerves and centers these visual organs become able to direct their own movements and those of the body. How the eyes arose as optic vesicles from the brain wall is an event recapitulated in the development of the nervous system in the young embryos of all true vertebrates (fig. 304). Thus there was added the region of the midbrain. Very early in phylogeny it acquired stability and remains as the permanent optic center in all higher forms. In the embryos of true vertebrates the development of the midbrain precedes that of the olfactory forebrain. It may be surmised that this early development of the eyes and optic centers also took place in phylogeny. The early stages of development in fish (fig. 304) and other vertebrates show the precocious development of the optic vesicles and the retarded appearance of the forebrain.

Lateral line organs appear in Petromyzonts, Fishes and larval Amphibians. In the region dorsal to the gills there appear in the skin certain pouches or vesicles. Their deeper parts, the placodes, come into close relation to the neural crest of the oblongata with which they establish nervous connection known as the lateral line, acoustic and vestibular nerves. The vesicles are transformed into the ear labyrinth and the lateral line canals which provide the animal with a mechanism responsive to changes of position and to vibrations in water which has become its habitat (fig. 304).

The forebrain arises as an olfactory organ at the rostral end of the neural tube. It is doubtful whether any true olfactory organ exists in the Amphioxus. The ciliated groove of Hatchek, the neuropore and the "wheel organ" suggest the likelihood of a chemical sense in this region designed to test the water for the presence of sapid substances in solution. No true forebrain is recognized in the Amphioxus although its terminal nerves which innervate the snout have been homologized with the terminal nerves of other vertebrates, and the infundibular organ (fig. 303, *inf o*) identifies the caudal part of the hypothalamus. The region in front of this is recognized as a primordium of the forebrain, or at least of the hypothalamus.

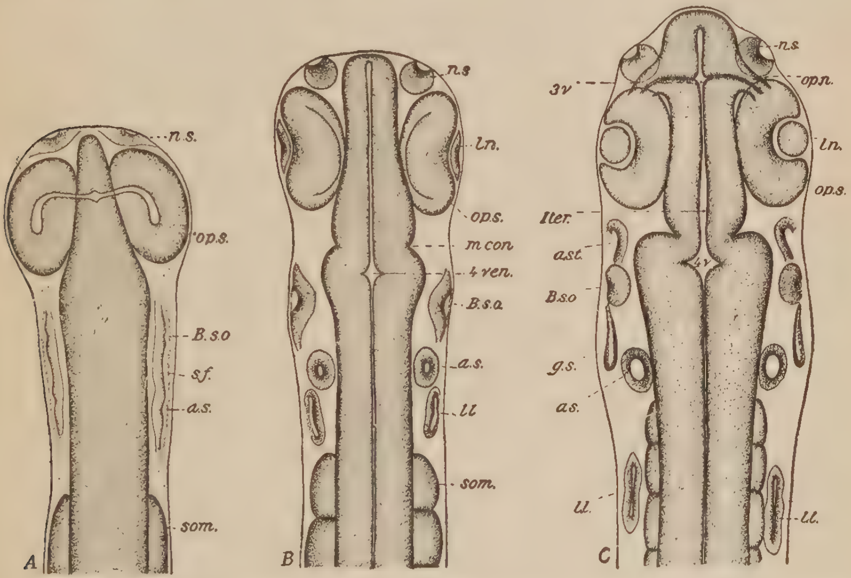


FIG. 304. *A. B. C.* Three stages in the development of the brain and sense organs in the sea bass. From H. B. Wilson. *a.s.*, auditory sac; *a.s.t.*, anterior sensory tract; *B.s.o.*, preauditory pit; *g.s.*, gill slit; *l.l.*, lateral line anlage; *ln*, lens; *n.s.*, nasal sac; *op.n.*, optic nerve; *op.s.*, optic sac; *s.f.*, sensory furrow.

The origin of the olfactory forebrain in true vertebrates was contingent upon the development of ciliated olfactory epithelium, sensitive to chemical excitations by sapid (protein) substances in solution in the water in which the animal lived (fig. 304, *n.s.*). These nasal sacs arose in direct relation to the end brain lateral to the terminal nerves and neuropore. Their mode of origin is comparable to that of the acoustic and lateral line placodes. By their stimulating influence they produced a forward growth of the brain tube with a decided tendency to evagination. The terminal nerves to the snout have remained as vestigial structures.

In all vertebrates the olfactory evagination occurs in front of the optic centers and tends to be lateral and double. Their terminal portions in connection with the olfactory vesicles form the olfactory bulbs, the basal portions form the olfactory lobes. A primitive median end-brain and interbrain unite the lobes with the midbrain or optic centers. Thus from the beginning the primitive forebrain consists of an unpaired ventricle common to it and the interbrain, and a pair of evaginations at the anterior end forming the two olfactory bulbs and ventricles. The forebrain of all vertebrates is formed on this fundamental plan. Though there is a diversity of detail in its differentiation in various forms, this fundamental plan remains unaltered. In every case this pair of evaginations furnishes the material out of which the olfactory brain and, ultimately, the cerebral cortex of higher forms are differentiated.

The forebrain of the Cyclostomes (fig. 298) represents an early condition in the formation of the olfactory brain. The lampreys and the hagfishes have developed a large suctorial mouth at their rostral end. Back of this they have a large double olfactory or nasal pit through which the water is pumped in and out by means of respiratory movements affecting the nasopituitary sac. In the developing larvae the close relation of the olfactory epithelium to the forebrain is evident. The small median end-brain is a forward continuation of the midbrain from which the optic vesicles are separated on each side. Not even in the adult lamprey are the olfactory bulbs fully evaginated but remain close to the nasal sacs. They constitute the front part of the olfactory lobes or primitive forebrain. On the lateral surface (fig. 298) a shallow sulcus indicates their caudal extent. The great suctorial snout and the dorsal position of the olfactory pit have further compressed the forebrain against the interbrain, but a deep sulcus marks the line of continuity of these two parts. The interbrain (or thalamus) is represented by the area of union and overlap of the visual brain and olfactory brain. The habenular nuclei seen on its dorsal surface and the inferior lobe or hypothalamic structures stand in direct fiber connection with the forebrain. Thus there is seen in the shortened brain of the Petromyzonts a very close relation between the partly evaginated forebrain, thalamus and midbrain.

The histological differentiation of the forebrain of the Petromyzonts is very primitive. There are, however, several well-defined tracts which put the olfactory brain in connection with the optic centers and with the centers in the region of the oblongata (fig. 300). The olfactory cells by means of the olfactory nerve (*oln*) connect with the cells in the olfactory bulb. From this numerous fibers pass backward into the olfactory lobe. The larger cortico-habenular bundle (*ch*) connects the olfactory lobe with the habenula (*hb*) and the habenulo-peduncular tract (*hp*) of Meynert in turn connects the habenula with the motor centers in the region of the bulb. Hypothalamic and subthalamic connections are also present. The striothalamic fibers (*olp*) connect the olfactory lobes with the ventral portion of the thalamus. There appears also to be an extensive connection of the lobe with the region of the bulb by the lobo-bulbar tract. It can be readily appreciated that such an arrangement of fiber connections enables the olfactory centers, primitive as they are, to excite the optic centers and particularly the bulbar centers where the more important reflex motor mechanisms are located. Thus olfactory excitations may influence the suctorial movements, and movements of the gills, or they may affect eye and bodily movements.

Professor Herrick says in this connection:

" The sense organs and peripheral nerves of cyclostomes are simply organized, but the pattern is in its broad outlines similar to that of the true fishes (Johnston, '05). Within the brain, however, the primary sensory nuclei into which the various sensory components of the cranial nerves (from skin, internal ear and lateral-line organs, taste buds, etc.) discharge their nervous impulses are far less sharply separated than in the true fishes. And in the higher correlation centers there is little precise localization of the functional areas. All forms of peripheral sensory excitation tend to converge into relatively few final common motor paths which are very simply arranged.

" From this arrangement of the conduction paths and nerve centers it follows that the nervous organization is such as to make possible a relatively small number of reactions to all sorts of sensory stimulation and that these reactions are for the most part simple total movements of the whole body rather than complex adjustments involving precise coördination of many separate organs. Observation of the behavior of Cyclostomes shows that this is, in fact, their type of reaction.

" This histological pattern of the Cyclostome brain is in sharp contrast with that of most of the true fishes and especially of the teleosts, where the various functional systems of neurons are segregated into as well-defined nuclei and fiber tracts as are those of the brain-stem of mammals. The histological pattern of the cyclostome brain may without question be regarded as typical of the primordial vertebrate ancestor. It is unspecialized, plastic, and capable of differentiation in any direction.

" It may be assumed that, if the Gnathostome vertebrates arose from some primitive extinct type of Cyclostome (as is the current belief), the cerebral histological pattern of this ancestral form was not more highly differentiated than is that of modern Cyclostomes."

The forebrain of Elasmobranch fishes represents the most typical form of the early vertebrates. The cartilagenous fishes are early aberrant fish forms that inhabit the deep waters. Their environment has never changed. The differentiation of their nervous system has remained along reflex lines. Locomotor, respiratory, visual and olfactory mechanisms have all been adapted to life, reproduction and seeking of food in water.

The snout is prominent, the terminal nerves are widely separated. The nasal pits are large and partially separated by two folds so that the respiratory movements maintain a current of water through them.

The olfactory bulbs (fig. 305) are widely evaginated and lie in close relation to the olfactory pits. There is a tendency for the bulbs to be double (quite pronounced in the rays) which is associated with the lateral elongation of the olfactory pits. More or less distinct medial and lateral olfactory nerves and tracts are differentiated in the thinned out olfactory stalk. The stalks expand into olfactory lobes which are evaginated considerably more than those of the Petromyzonts.

Behind these there is still a considerable amount of unevaginated end brain which connects the olfactory centers with the thalamus and midbrain. Along the midline the terminal portion represents a considerable thickening and union between the olfactory lobes (fig. 305). The histological structure of the selachian forebrain shows the differentiation of a considerable number of nuclear masses related to the incoming olfactory tracts. The arrangement of the tracts and centers is much more precise than in the more generalized Petromyzonts. From figures 294 and 295 it will be seen that the fiber connections of the forebrain are comparable to those of Petromyzonts (fig. 300) and bony fishes (figs. 296, 297).

The olfactory nerve filaments connect the mucosa to the olfactory bulbs. The mitral cells of the bulbs project the olfactory tracts fibers (fig. 295, *op*) which spread out and end in the anterior, ventral and lateral walls of the olfactory lobes which constitute the forebrain. The ventral wall forms the medial olfactory nucleus (*tub. olf.*) which appears to be the primordium of the olfactory tubercle of higher forms. It is continued into the medial wall which is more or less closely united with that of the other side (fig. 305) to form a septal region. In this medial wall, olfacto-septal fibers from the region of the tubercle are projected dorsally to end in the dorsal wall of the forebrain. For fiber connections see (figs. 294, 295). The more important connections from the region of the olfactory tubercle are fibers that pass backwards in the medial forebrain bundle (*f. med. t.*) to end in the hypothalamic region and also the olfacto-habenular tracts (*oh.*).

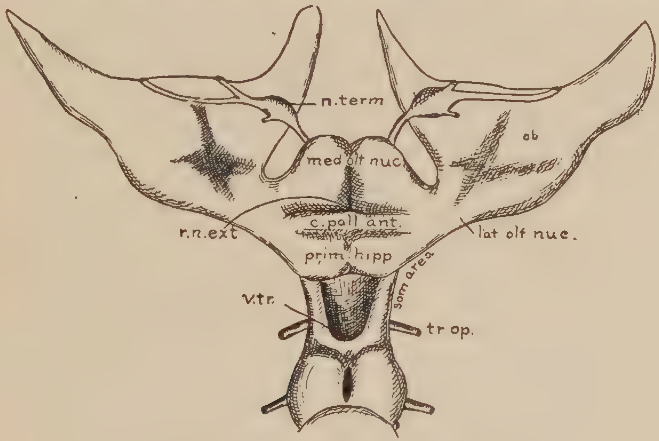


Fig. 305. Forebrain of a shark, *Scyllium stellare*.
From J. B. Johnston. Jour. Comp. Neur. **21**.

In the dorsal medial walls (*a. ol. d.*) there has been identified the primordium of the hippocampus of higher forms. These walls are connected with the medial area by the olfacto-septal fibers, with the lateral area by short fibers, and with the hypothalamus by the tractus pallii. They project fibers on the hypothalamus comparable to the fornix (*c.f.*), and on the habenula, fibers comparable to the cortico-habenular tracts (*ch.*) of higher forms. According to Johnston and others the tractus pallii also contains the ascending (gustatory) fibers from the hypothalamus.

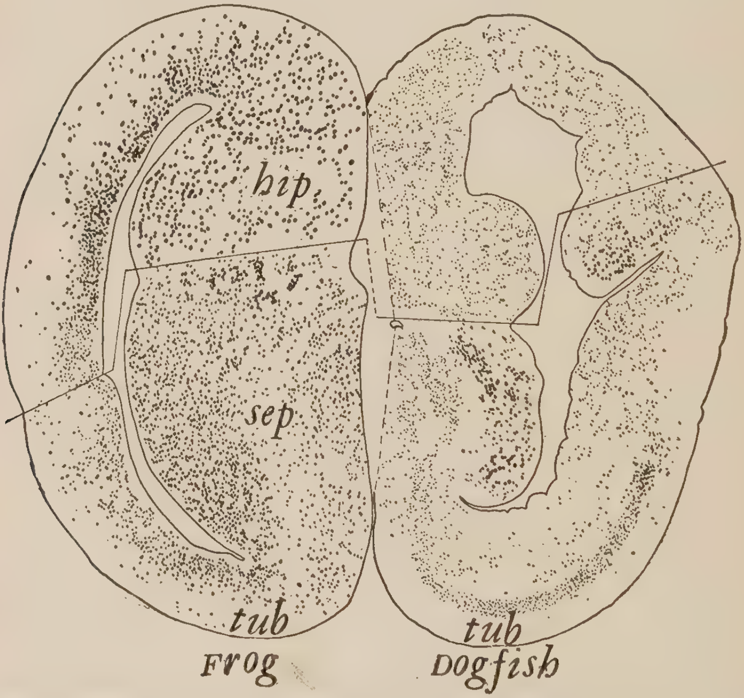


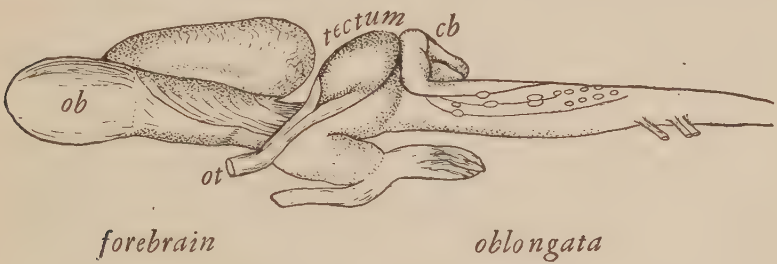
Fig. 306. Cross section of the forebrain of a frog compared with that of a dogfish. Note the homologous parts. From J. B. Johnston.

The close resemblance of the nuclear masses in the medial wall of the forebrain of a dogfish to those of a frog may be seen in figure 306.

That the caudal part of the lateral wall (*a. som.*) of the forebrain receives also afferent connections from the thalamus has been stated by Johnston. He has identified this region as the primitive somatic striatum. Thus the thalamic tract (*tr. th. f.*) may represent such a connection and may correspond to the fasciculus thalamicus and anterior peduncle of the thalamus of higher forms. Fibers from the striatal area (*a. som.*) are also sent down (*tr. som. p.*) and represent a primitive striopeduncular tract.

Thus in the Selachians the medial and lateral olfactory areas have relations and fiber connections which make them directly comparable to structures such as the olfactory tubercle, the lateral olfactory area and striatum of higher forms. A rudimentary dorsal medial structure has also appeared which from its connections may be considered the forerunner of the amygdala and the hippocampal formation.

A comparison of the Elasmobranch forebrain with that of the Amphibia shows that the caudal part of the forebrain of these fishes is poorly developed especially in the lower types. In the Amphibia the early evagination of the caudal part and its close relation to the succeeding parts of the brain are noteworthy differences, and are suggestive of conditions seen in the Petromyzonts.



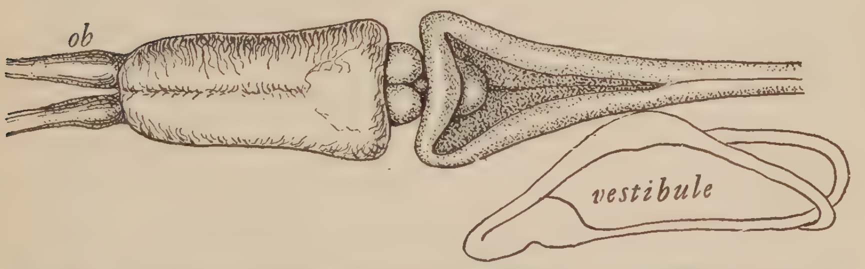


FIG. 307. The brain of the Congo river mudfish, *Polypterus bichir*, 62 cms. long, × 3.
FIG. 308. The brain of the Ganoid fish, *Polypterus bichir*, 28 cm. long, × 4½. The vascular membrane has been removed. After Bing and Burkhardt.

The forebrain of Ganoid fishes (fig. 296) shows a specialization in the direction of bony fishes. In Polypterus the olfactory bulbs are fully evaginated (fig. 307) and the primitive end brain is elongated. The side walls are massive and everted (fig. 312) but the roof is formed by a thin undifferentiated membrane depressed along the midline so as to give the appearance of a double end-brain behind the terminal plate; but no part of the forebrain is evaginated except where it joins the bulbs. Polypterus is more definitely Teleostean than an Amphibian ancestor.

Other Ganoids, such as the sturgeon, acipencer (fig. 309) possess evaginated brains closely resembling those of the cartilaginous fishes. The olfactory bulbs are largely evaginated in front of the terminal end plate. Most of the primitive forebrain is still a common unevaginated median structure. The lateral walls are greatly thickened by the growth of special nuclei.

The forebrain of the Teleosts or bony fishes (figs. 286, 290, 296, 297) is highly specialized through its connections with lower reflex centers. The olfactory lobes are only partly evaginated but their basal and lateral walls are very thick, due to the great specialization of the olfactory centers. The roof has remained membranous and is stretched over the greatly enlarged basal parts. The specialization of forebrain structure that began in the fresh water Ganoids has gone the limit in the Teleosts. These active forms became the dominant fresh water fishes and now compete with the Elasmobranchs in salt waters. The greatly developed optic centers, the valvula of the cerebellum which has invaginated the optic lobes and also the striatal structures have all contributed to the success of this type of fishes. In comparison with these structures the olfactory

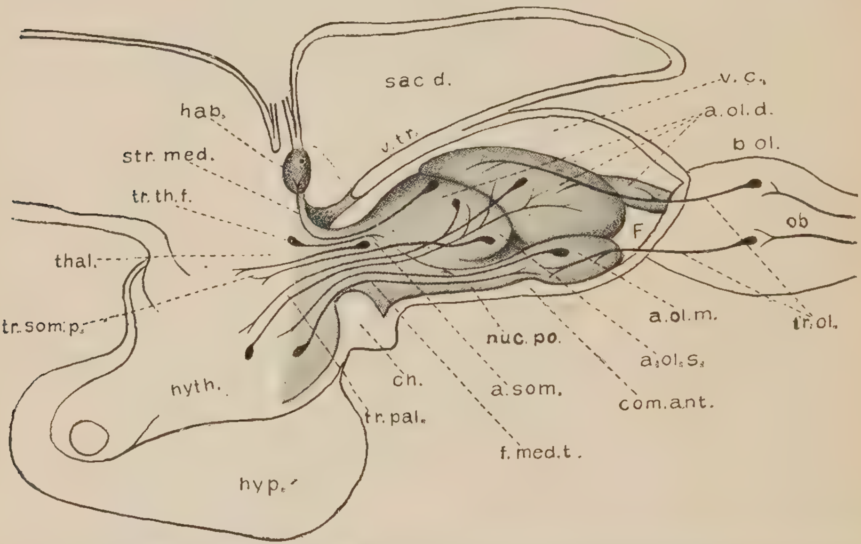


FIG. 309. Diagrammatic median section and main fiber tracts of the forebrain of the lake sturgeon, *Acipenser r.* Based on figures and descriptions of Johnston. From C. J. Herrick.

forebrain has remained rudimentary and appears dwarfed in size. There is no indication in the forebrain of Teleosts of further evolution in the direction of the Amphibian or Reptilian types. The fiber connections of the teleostean brain (fig. 296) are more complex and specialized than those of the Selachians.

The forebrain of the Dipnoi or lung fishes (fig. 310) has the typical hollow thin wall evaginations that are found in the Amphibians. The brains of the two lungfishes, protopterus and lepidosiren, resemble each other. At the rostral end are the pointed olfactory bulbs (fig. 310, *ob*) closely connected with the tubular olfactory lobes.

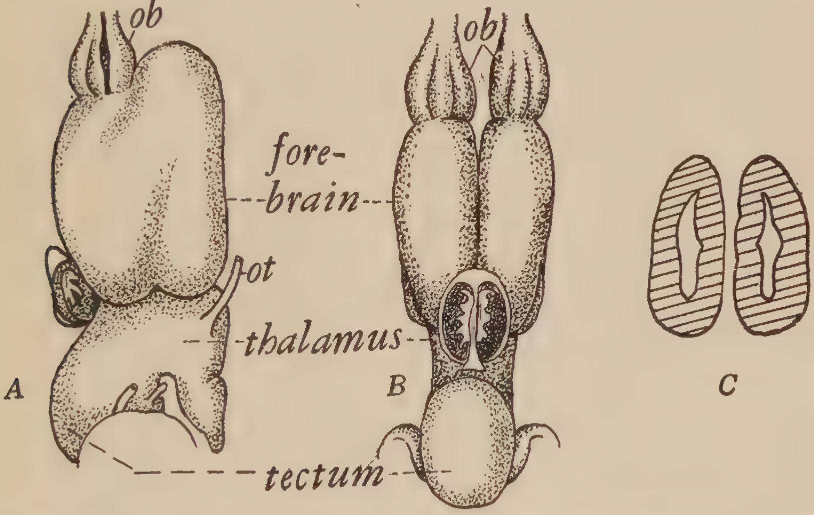


Fig. 310. The forebrain of the African lungfish, *protopterus annecteus*. *A*, dorsal view; *B*, lateral view; *C*, schematic cross section.

The lobes project forward and far beyond the terminal plate, which indicates a state of advanced evagination found typically in all higher vertebrates. What is known of the histological structure of the dipnoian forebrain indicates a condition which does not follow the line of differentiation of the cartilaginous and bony fishes. In general features these forebrains resemble more those of the necturus and other larval Amphibia.

The dorsal wall of the forebrain vesicle of lepidosiren (fig. 311) contains a compact layer of cortical cells. The lateral wall is specialized to form a rudimentary piriform area into which fibers of a definite lateral olfactory tract pass. The dorsal portion of the medial wall forms a primordium hippocampi. It receives fibers from the anterior and medial regions of the forebrain. The cells of the primordium hippocampi give rise to the fornix fibers which pass ventrally through the septal region to end in the hypothalamus.

The ventral wall is so highly developed that the olfactory tubercle forms more than half the forebrain hemisphere. The tubercle receives fibers from the olfactory bulb. On its ventricular surface it is thickened to form the olfactory striatum. The thickenings that constitute the striatum are connected caudally by striothalamic and striopeduncular fibers.

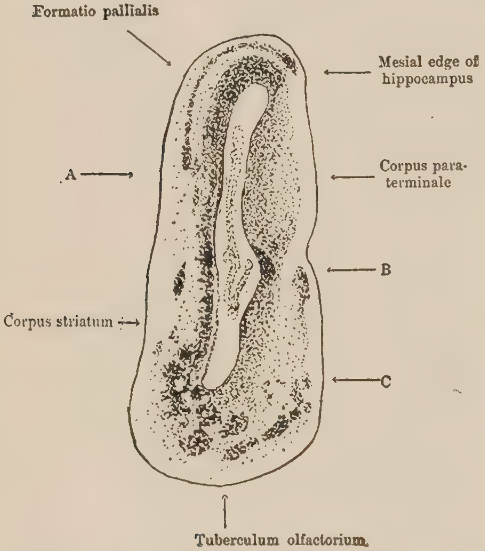


FIG. 311. Cross section through the left forebrain vesicle of an adult *Lepidosiren paradoxa*. From G. E. Smith.

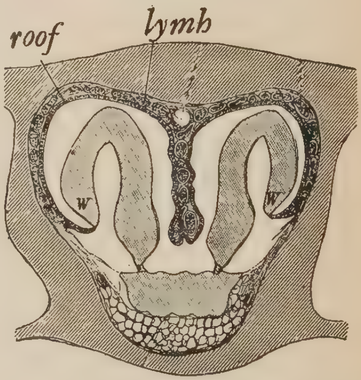


FIG. 312. Cross section of forebrain of *polypterus b.*, showing eversion of lateral walls and a membranous roof like other Ganoids. From Waldschmidt.

It will be seen that this Dipnoian brain resembles in a remarkable way the forebrains of Amphibia and Reptiles.

The forebrain of Amphibians (figs. 254, 261) is a double fully evaginated tubular structure whose origin appears to be from forms resembling the lungfishes. From paleontological evidence it appears that the ancestors of Amphibia were primitive Ganoids of the general type resembling polypterus. It has been pointed out by Professor Herrick that the resemblance of the forebrain of lepidosiren and protopterus to that of the generalized Amphibia is very close, and that it is therefore very probable that the primitive Ganoidean ancestor of the Amphibians had a forebrain closer to that of protopterus than to any other surviving type. Modern Amphibia are, it is true, aberrant forms and some like necturus are probably regressive forms. But the larvae of all amphibian species are similar and furnish reliable information on amphibian ancestry. Then, too, the adults of various species illustrate arrests of the developmental process at various stages. For example, the adult necturus appears to be an immature Amphibian. Its histological pattern is similar to that of other amphibian larvae and more to that of the adult Cyclostomes than to that of the fishes. Even in the regions of the midbrain, cerebellum and oblongata this resemblance is evident.

Professor Herrick has pointed out that these Amphibians preserve both in form and in histological structure a young or undifferentiated type which is more plastic and has greater potentialities for evolution in the new direction taken by the Amphibians and their derivatives who have taken up a habitat in mud and shallow water of inland regions.

The forebrain of Amblystoma illustrates the special features of Amphibian forebrain morphology (figs. 261, 262). Each half is fully evaginated, is elongated and its terminal end forms the olfactory bulb in which the olfactory nerves end. This is not separated from the olfactory lobes as in protopterus. Posteriorly the lobes are closely united with the midbrain by a fairly well-defined interbrain or thalamus. Medially they are united with each other by the terminal lamina in front of the optic chiasma and interventricular foramen. The walls are thickened but not everywhere alike. In the dorsal medial wall appears the primordium hippocampi; ventrally are the nuclei septi. In the ventral wall are the striatal nuclei and laterally the olfactory area, while the dorsolateral wall, not so highly differentiated, stands in relation to fiber systems that reach it from more caudal parts of the nervous system. Thus this lowly Amphibian forebrain contains the primordium of the essential parts found in the reptilian and the more highly developed mammalian brains.

In Amblystoma larvae the evagination of the forebrain does not begin at the site of the future olfactory bulb but at the caudal end in front of the velum as in lepidosiren. This caudal evagination is well under way before the evagination of the olfactory bulbs takes place adjacent to the nasal sac. It thus seems that some other factors besides the nasal sacs have played a part in moulding the growth of the cerebral vesicles of the Amphibia. These factors may be present to a slight degree in Cyclostomes and in some Selachians and not at all in other fishes.

The forebrain of the frog (fig. 258) shows a similar condition of development. The olfactory nerve (*oln*) is connected with the olfactory bulb which is formed by the anterior part of the forebrain tube. On the lateral surface the lateral olfactory tract (*lot*) passes to the more posterior part of the forebrain vesicle. The walls of this vesicle are divisible into three parts — a ventral region (*tub*), a lateral wall (*pir*) and a medial wall in which the hippocampal structures are formed. The presence of these structures constitute a definite step in the upward evolution of the amphibian forebrain even though the brain of the frog is markedly undeveloped in its striatal and cerebellar structures.

The fiber connections of the Amphibian forebrain are shown in figure 257. It will be seen that the olfactory nerves (*oln*) end in the olfactory bulbs which form the front tip of the forebrain. These have a structure (fig. 263) comparable to those of the fishes as well as those of the lower mammals (fig. 183). The olfactory peduncle (*op*) is a continuation of the tubular bulb backwards into the forebrain vesicle as in Reptiles and Mammals. Its tubular walls which contain less differentiated cellular regions (*ant olf nuc*) merge insensibly with the walls of the forebrain. The diffuse olfactory tracts connect the bulbs with the ventral region of the olfactory tubercle (*tub*) and the lateral region or piriform area (*pir*). Other fibers pass to the ventral part of the anterior commissure (*ac*) and reach the bulb of the other side.

A large tract of olfacto-peduncular fibers (*olp*) comes from the anterior region of the tubercle and passes over the optic tract to end in the hypothalamus. In the medial wall the olfactoseptal fibers (*ols*) connect the ventral and medial olfactory regions with the dorsal medial wall which may be regarded as the precursor of the gyrus dentatus and hippocampus of the higher forms. Professor Herrick has identified in the medial wall a small fornix bundle (*fx*) and fibers that form a hippocampal commissure (*fxc*) just dorsal to the anterior commissure. Fibers (*ch*) from the medial wall as well as fibers (*oh*) from the olfactory tubercle (*tub*) and preoptic nucleus pass backward to end in the habenular nuclei, from which the habenulo-peduncular tracts (*hp*) are projected down to the inter-peduncular region.

The lateral wall of the forebrain which contains the lateral olfactory nuclei, the primitive somatic striatum, the piriform area and the amygdala receives the endings of the lateral olfactory tract. It is connected with the opposite side by the anterior commissure. It is connected downwards with the thalamic region by means of the lateral forebrain bundle which consists of the descending strio-peduncular (*stp*) and strio-tegmental (*stt*) tracts, and also ascending fibers (*ft*) from the dorsal part of the thalamus. As in higher forms a diagonal band (*db*) of fibers connects the surface of the lateral olfactory region with the medial surface.

The forebrain of Reptiles shows a definite increase in size and specialization of its walls (fig. 216). The olfactory bulbs (*ob*) are more distinctly set off, but still form the front tips of the forebrain evaginations. In some forms a distinct coronal sulcus marks the ring of union between the bulbs and the forebrain vesicles.

The **olfactory tubercle** forms the greatly thickened and enlarged ventral wall. It is covered by a specialized cortex invaded by large numbers of ventral and medial olfactory tracts. Within the tubercle there is differentiated a greatly thickened mass, the **olfactory striatum** (*ost*). It has also been designated paleostriatum on account of its phyletic antiquity, for its evolution can be traced to a similar structure in Amphibia, Dipnoi and Fishes. This elevation can be well seen in the floor of the ventricle (fig. 221, *ost*). In a section taken across this region (fig. 232) it is seen that the tubercle and olfactory striatum on the lateral side join the piriform area. On the medial side they extend upward in the medial or septal wall for a short distance. At their posterior parts the tubercle and striatum are connected with the other side by the anterior commissure.

The medial forebrain bundle (figs. 235, 236, *mfb*) forms a prominent connection between the olfactory striatum and septum, and the thalamic region. It consists of both descending and ascending fibers. The descending olfacto-peduncular tracts (*olp*) arise from the olfactory striatum and pass down to end in the hypothalamic region. The ascending fibers form the anterior peduncle of the thalamus (*apt*). They arise from the medial nucleus of the thalamus (*med*) and adjacent nuclei, and extend forward into the region of the septum. Other fibers connect the septum with a small dorsomedial nucleus of the thalamus (*dmn*) which lies in relation to the medullary stria. Olfacto-septal fibers (*ols*) from the posterior region of the olfactory tubercle pass upward into the septum and enter the superficial layer (dentate gyrus) of the hippocampal formation.

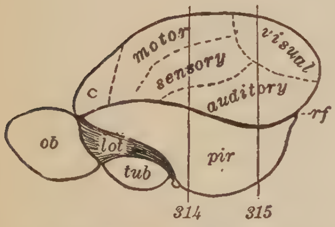
The **somatic striatum** or epistriatum is another elevation in the ventrolateral wall of the forebrain. It is homologous to the putamen, caudate nucleus and globus pallidus of higher forms and to the somatic area of Fishes and Amphibians. It is connected with the thalamus by a large tract, the lateral forebrain bundle (*lfb*), which corresponds to the thalamic fasciculus (*tf*), the ansa lenticularis (*ansa*) and some of the posterior thalamo-cortical radiations (*sr*) of higher forms. The strong connections that the lateral geniculate body (*lg*) and the important nucleus rotundus make upwards with the somatic striatum is one of the most important features of the reptilian brain. It seems likely that the ascending tracts in the medial and lateral forebrain bundles pass to the thin brain wall beyond the striatal bodies, at least in some reptiles. The phylogenetic forerunners of the lateral forebrain bundle appear to be the lateral strio-thalamic tracts and tractus pallii of Amphibians and Fishes. The ventricular eminence of the somatic striatum arises as a great infolding of the cortex along the lower border of the piriform area (fig. 232). Its layer of cells is in continuity with that of the piriform area and that in turn with that of the dorsal brain wall.

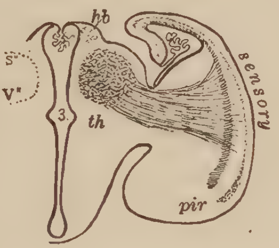
The **amygdala** (*amy*) is the thickened cortex that forms the posterior ventral tip of the brain in relation to the somatic striatum. It corresponds most closely to the ancient lateral olfactory nuclei and striatum of Fishes, of which it seems to be a phyletic residue. It is connected with the hypothalamic regions by tracts which pass in the groove between the striatum and the thalamus.

In the lateral wall a large band of lateral olfactory fibers (*lot*) connects the bulb with the lateral and posterior wall of the forebrain. Along the line of this band the cortex of the lateral wall is specialized to form a rudimentary piriform area (*pir*). This appears definite for the first time in the Reptiles though its rudiment can be recognized in the Amphibia.

The **hippocampal formation** (*dg*) forms the thin dorsal and medial wall of the forebrain. In most reptiles the typical inflexion of the hippocampus has not taken place. The hippocampal formation consists of three layers. The outer layer receives a diffuse tract of fibers (*ols* and *sh*) from the anterior and medial brain wall and septal region. The second layer consists of the small pyramidal cells of the dentate gyrus (*dg*) and hippocampus (*hip*) whose fibers form the innermost or third layer called the alveus. The fibers of the alveus also come from outlying cortex adjoining the piriform area.

The fibers of the alveus form two bundles, the fornix (*fx*) and the angular bundle (*ang*). The fornix fibers (*fx*) pass ventrally in the medial wall through the septum to reach the hypothalamus and habenula. The fibers of the angular bundle arise from the piriform cortex and pass to the other hemisphere forming the hippocampal or posterior pallial commissure. It is through this system of fibers that the piriform cortex of one side comes into functional relation with the hippocampus of the other side. A smaller septal commissure (*fxc*) or dorsal commissure is another one that occurs in the septal region dorsal to the anterior commissure. In many reptiles it is large (fig. 220, *fxc*) and contributes to the anterior commissure.





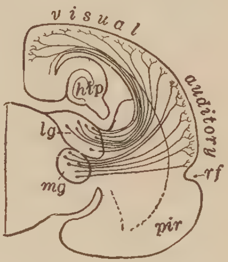


FIG. 313. A map of the cortical areas of a primitive mammal. After G. E. Smith. The plane of figures 314 and 315 is indicated by the vertical lines.

FIG. 314. Section across the right side of the forebrain of a fetal platypus showing the directness of the sensory tract from the thalamus to the sensory area of the cortex. The platypus has a large sensory bill and the trigeminal nerves and centers are very large.

FIG. 315. A schematic section through the caudal part of the forebrain showing the direct topographical projection of the optic and auditory centers of the thalamus (*lg*, *mg*) on the visual and auditory areas of the cerebral cortex. After G. E. Smith.

The **optic tracts and centers** of Reptiles and Birds are also greatly enlarged and developed.

The forebrain of a Monotreme (fig. 49) or a marsupial can be directly compared with that of the Reptiles. The olfactory bulbs, lateral olfactory tracts, piriform area and dorsal cortex are greatly enlarged. The olfactory tubercle, the olfactory striatum and somatic striatum have relations and structure comparable to those seen in the Reptiles. How closely the medial wall, the olfactory tubercle and the striatal bodies correspond to those of the Reptiles and lower vertebrates can be seen from a review of figures 51, 52, 218, 232, 259, 262, 264, 306. The real difference is found in the greater size of the cerebral cortex of the mammals.

Definite thalamo-cortical connections are not conspicuous in the Reptiles. Though a number of thalamic nuclei and thalamo-striatal tracts exist, the extent to which their fibers invade the lateral brain wall beyond the striatum and piriform area is nevertheless very limited. In respect to this one feature, the brains of the Monotremes and Marsupials present the most marked advance over their kindred, the Reptiles.

The basal forebrain bundles in the Mammals are greatly enlarged by the accession of these thalamo-cortical connections which are now spoken of as the **internal capsule** (*int*) and **cerebral peduncles** (*cp*); and the regions of the cerebral cortex which these fiber tracts reach beyond the striatum have undergone considerable growth in extent.

Professor G. E. Smith has shown that there is a definite topographical relation between the regions of the thalamic nuclei and the regions of the cortex which their fibers reach in these lowly Mammals (figs. 313, 314, 315). Thus the visual centers in the posterior portion of the thalamus called the lateral geniculate nuclei (*lg*) project fibers upon the adjacent occipital region. The more ventrally situated auditory center, the medial geniculate nucleus (*mg*), projects fibers on the ventral, lateral wall. The anterior lateral nucleus projects fibers on the dorsal portion of the brain wall. The large medial trigeminal nucleus projects fibers on the ventral anterior portion of the brain wall. These relations are well demonstrated in the platypus in whom the trigeminal nerve and thalamic centers are greatly developed in connection with its highly sensitized bill. Out of these sensory connections arose the areas of the mammalian cerebral cortex which have undergone enormous amplification in the gyrencephalic mammals. For further details see Chapter 32.

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